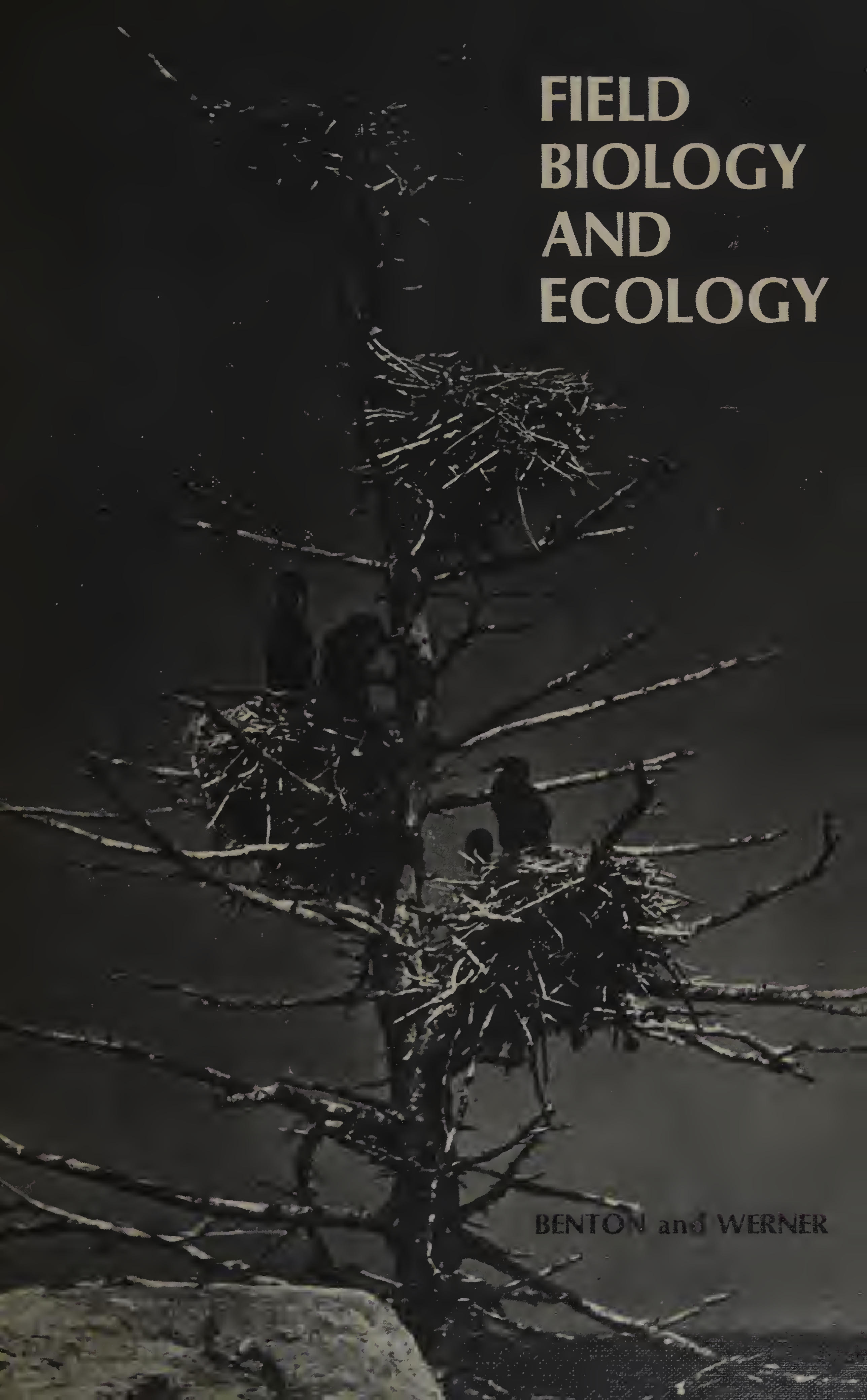
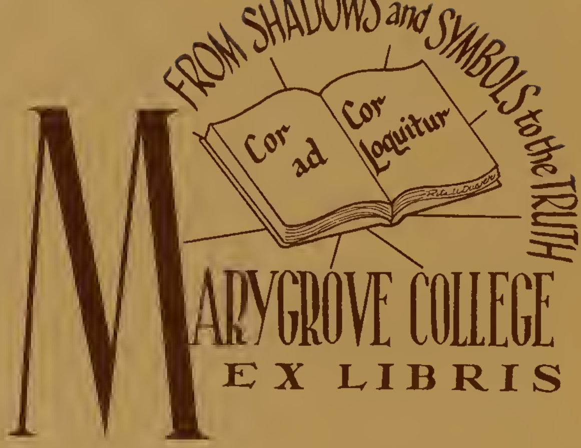
FIELD BIOLOGY AND ECOLOGY

BENTON and WERNER





FROM SHADOWS and SYMBOLS to the TRUTH
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Field
Biology
and Ecology

Field Biology and Ecology

Second Edition

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FIELD BIOLOGY AND ECOLOGY

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Preface

Up to a century ago, most of the great biologists were field workers and were known as naturalists. Their studies were based largely on field observations or on data collected by assiduous field work. The latter years of the nineteenth century and the early years of the twentieth brought about the ascendancy of the laboratory aspects of biology—genetics, physiology, anatomy, and the like—and the naturalist passed into relative oblivion. Work in the field, with uncontrolled nature, was considered by many scientists to be hardly worthy of the true scientific biologist, who wanted controlled experiments. As a result, the laboratory sciences made tremendous strides, while advances in the knowledge of the life and habits of organisms were slow.

About the beginning of this century, events brought about a change in the importance of field biology. The rise of ecology, the increased need for conservation of natural resources and for management of wildlife, and the tremendous upsurge in popular interest in nature study have combined since that time to send thousands of workers into the field. Some are professionals; many are amateurs. Today there are fifty bird watchers in the city parks for every one who was there a half century ago. Amateur biologists pursue lizards over the deserts of Arizona, watch at a wren's nest in Illinois, and collect marine plants and animals on Cape Cod. Conservation workers count deer herds in Michigan and evaluate grouse cover in New York. Ecologists measure the temperature and humidity of gopher burrows in Utah and count plants on square meters of ground in every state of the Union.

Field biology has become the biology of the people, the science of life as it exists everywhere, which everyone can study and everyone can enjoy. It is well that this is true; for as faith without works is dead, so are works without faith. Conservation, ecology, and all other phases of biological research depend for their existence upon the faith and support of an enlightened public. And the surest progenitor of this faith is a consuming interest in, and an adequate knowledge of, nature. It is the purpose of this book to contribute to the stimulation of such interest and to the dissemination of such knowledge of the principles and practices of the field aspects of biology.

As a textbook, this book is designed to meet the needs of the beginning ecology or field biology course. It is assumed that the student will have taken a minimum of six hours of introductory biology courses as a prerequisite. A workbook which complements the text in field and laboratory use is printed by the Burgess Publishing Company, Minneapolis.

In the six years since the appearance of the first edition of this book, the branches of biology with which it is concerned have not been standing still. A surge of interest in ecology has resulted in a wealth of new information about energy relationships, behavioral ecology, oceans and their organisms, physiological ecology, biogeography, and other aspects of this vast area of knowledge. New theories, refined techniques, and advanced instrumentation have played a part in this explosion of scientific information.

While all this has been going on, we have been informed by many colleagues and users of our book about its numerous shortcomings. In preparing a second edition, we are humbly grateful to the numerous reviewers and critics, formal and informal, from whom we have gleaned ideas which are used herein. The entire text has been carefully reviewed, and most of the chapters rewritten. We have thought it desirable to add chapters on energy relationships and marine ecology, while attempting to integrate recent information in other areas into already existing chapters. The Appendix has also been thoroughly revised to include references to recent publications and to increase the usefulness of the sections on techniques and others.

It would be impossible to acknowledge all those who have helped us in the preparation of this book. Our colleagues in the teaching of biology, particularly those at the State University of New York at Albany, have assisted us from the outset. Portions of the manuscript have been read and criticized by Taylor Alexander, John Belknap, Lawrence Bliss, Maxwell Doty, Frank Egler, Reed Fautin, Mabel French, Lucille Grace, Joel Hedgpeth, Violet Larney, Paul C. Lemon, Hilary B. Moore, Ralph S. Palmer, Daniel Smiley, Lowell D. Uhler, Robert Whittaker, and the late Alvin G. Whitney. For permission to use illustrations, we are indebted to Richard Axtell, Victor Cahalane, Maxwell Doty, Frank B. Golley, Alan Heath, Joel Hedgpeth, Lloyd C. Ingles, C. E. Lane, Ralph S. Palmer, Olin S. Pettingill, Jr., Frank Pitelka, Thola Tabor Schenck, Minnie B. Scotland, N. Tinbergen, H. Wayne Trimm, Allan Tucker, J. R. Vallentyne, Ecological Monographs, The Oxford University Press, New York, Prentice-Hall Inc., Englewood Cliffs, N.J., Charles Scribner's Sons, New York, The United States National Park Service, the United States Soil Conservation Service, the New York State Conservation Department, and the Newfoundland Department of Mines, Agriculture, and Resources.

Our students have, for many years, been unwitting guinea pigs for much of the information which has found its way into the book, as well as for much which has been left out. Special thanks are due to our department heads, Dr. Paul C. Lemon, Dr. Minnie B. Scotland, and Dr. Willard F. Stanley, for assistance and encouragement of many kinds. We are indebted to Blackburn College for secretarial help in the preparation of the manuscript.

Most important of all has been the patient forbearance of our wives, who have suffered through long periods of being "book widows" without complaint.

Allen H. Benton
William E. Werner, Jr.

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Field
Biology
and Ecology

chapter 1

What, why, and how

The study of biology is the study of life. As living beings ourselves, we are naturally inclined toward the study of life in its many interesting aspects. We may want to know the names of the animals and plants around us, so we must learn the principles of *taxonomy,* the naming of organisms. We may want to learn more about the way in which life's functions are carried on, so we study *physiology.* We may wonder how a particular organism or species gets along with its neighbors in the wild, so we study *ecology,* a branch of biology which is concerned with organisms in relation to their environment. Or we may study *ethology,* animal behavior; *anatomy,* animal or plant structure; *genetics,* the study of heredity; or any of the many other branches of biology. The study of life, in one form or another, has almost universal appeal.

We may think of *field biology* as the study of life under natural conditions or in its natural habitat. Much of ecology is thus included in the broad area of field biology, while a large

It is a monstrous abuse of the science of biology to teach it only in the laboratory. . . . Life belongs in the fields, in the ponds, on the mountains and by the seashore.

James G. Needham

part of the rest, especially physiological ecology, is a laboratory discipline. As opposed to this and other strictly experimental disciplines, field biology is first observational and secondarily experimental. Instead of removing organisms from their native environment to study them in the laboratory, we go where they are and observe them there (Fig. 1-1). If we cannot make the necessary observations or perform the desired experiments under natural conditions, we may try to duplicate natural conditions as nearly as we can in the laboratory, where certain factors may be controlled.

The profession of field biology, or its amateur status as a hobby, is an ancient and honorable one. Whether we begin with Noah, who must have had a sound knowledge of animals to select his breeding stock wisely, or with Aristotle, the first field biologist whose written work has come down to us more or less intact, we will find a noteworthy line of men of many countries: Gilbert White, the gentle old vicar of Selborne,

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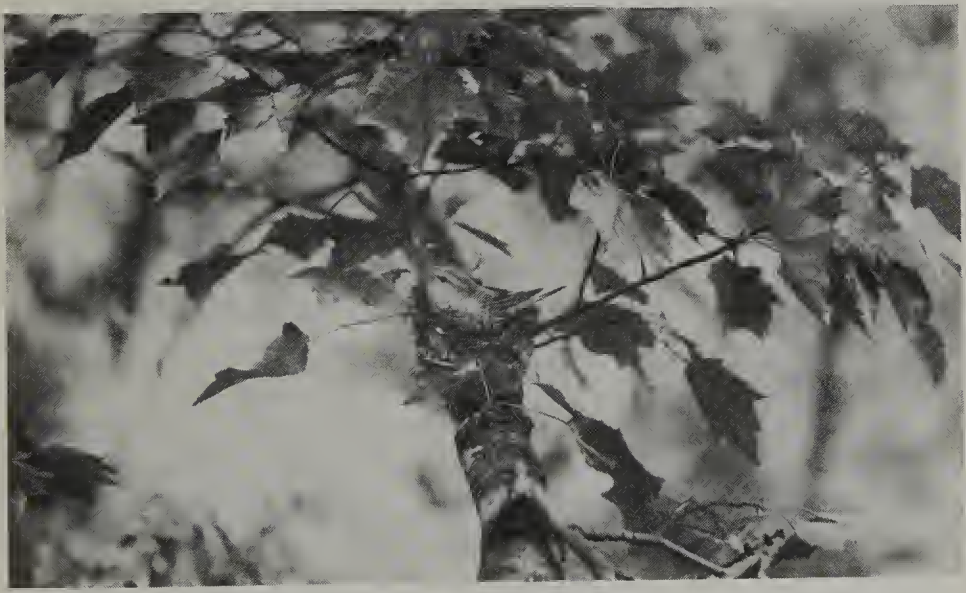
Fig. 1-1 A group of field biology students conducting a salamander census.

whose letters on nature have become literary classics; Jean Henri Fabre, the incomparable observer of insects, whose work is still read with pleasure and profit; Carl von Linné, who as Carolus Linnaeus became the world's greatest classifier; John Bartram, the Quaker naturalist and explorer, whose home was the center of science and culture in young America; all these and many others from antiquity to the present have contributed to the development of field biology (see Peattie, 1936).

From the purely personal point of view, the aesthetic value of field biology is sufficient to justify its existence as a hobby, if not as a profession. He who listens to the twilight song of the hermit thrush, or thrills to the lonely wail of the coyote, or watches the primeval courtship of salamanders in the midnight darkness of the spring ponds, stores up riches of the mind which neither time nor circumstances can destroy.

Yet amateur field biologists need not find their hobby a lonely one. No professional can cover an area as thoroughly as one who knows it, loves it, and lives in it day by day. Stations of rare plants may be discovered by amateurs as readily as by professionals. Amateur observers have made and continue to make great contributions to the study of birds (Fig. 1-2). Even the sleek, sinuous beauty of snakes and lizards has a peculiar attraction for some of us who can see the beauty of perfect function as well as beauty of form and color. Were there no other value than the purely aesthetic or the purely scientific in the study of nature, its pursuit would be amply justified.

Wherever we look, however, we see the beneficial results of field biology. Control of noxious insects, for example, is now a billion-dollar business, to which each of us contributes through his taxes. Besides its direct effect on our pocketbooks, insect control has an equally important relationship to our very survival. On the one hand, we must live on the products of our farms and forests, where the front line of the battle between insects and man is formed. The development of new chemicals to combat harmful insects is the duty of the chemist, and he has done his job wonderfully well. The new insecticides are fearfully effective. But only the field biologist can adequately supervise the use of these chemicals. It is short-



Verdi Burtch

Fig. 1-2 The cerulean warbler, *Dendroica cerulea,* on its nest. The photographer was an amateur naturalist who contributed many papers to professional journals.

sighted indeed to poison a field for the purpose of killing grubs if the treatment will destroy the earthworms and other soil organisms which help to keep the soil fertile; worse, the poison may be ingested by livestock and thence transmitted into meat or milk for final ingestion by human beings (see Carson, 1962).

Often the field biologist can develop controls which are effective against pests but which do not require chemicals. Such biological controls are more effective in the long run, although more difficult to put into effect. A few years ago the pea aphid in parts of the East was brought under control by the importation of lady beetles after chemical controls had failed. Other attempts at biological control by importation have been less successful owing to lack of information. The introduction of the mongoose to some of the West Indies to control rats resulted in the near extermination of native ground-nesting birds, while rats continued to flourish. From a small original introduction into Australia, the European rabbit grew into a population of 1 to 3 *billion.* After all attempts at shooting, poisoning, and other control methods had failed, biologists introduced a virus which causes a disease known as myxomatosis. The disease is highly fatal to rabbits but does not appear to harm other animals. It is transmitted by mosquitoes and is thus self-perpetuating. In early experiments, a 99.5 per cent kill of rabbits was secured in some areas (Herman, 1953). The disease has since been introduced into Europe accidentally and has similarly decimated the European rabbit population.

Not all importations, however, are unfortunate ones. The bird's-foot trefoil was accidentally introduced into this country and has adapted itself so well to poor soils that it is widely grown as a forage crop on soil too poor to grow alfalfa (Fig. 1-3).

Field Biology and Ecology

In the young science of ecology, the field biologist has always had a leading part. Ecology is the more sophisticated offspring of the old natural history; indeed, one ecologist (Adams, 1917) has called ecology "the new natural history." Only by careful observation and study of nature and intimate knowledge of the lives and habits of wild organisms can ecological data be properly gathered and correctly interpreted. Today, much of ecology has become a laboratory science.

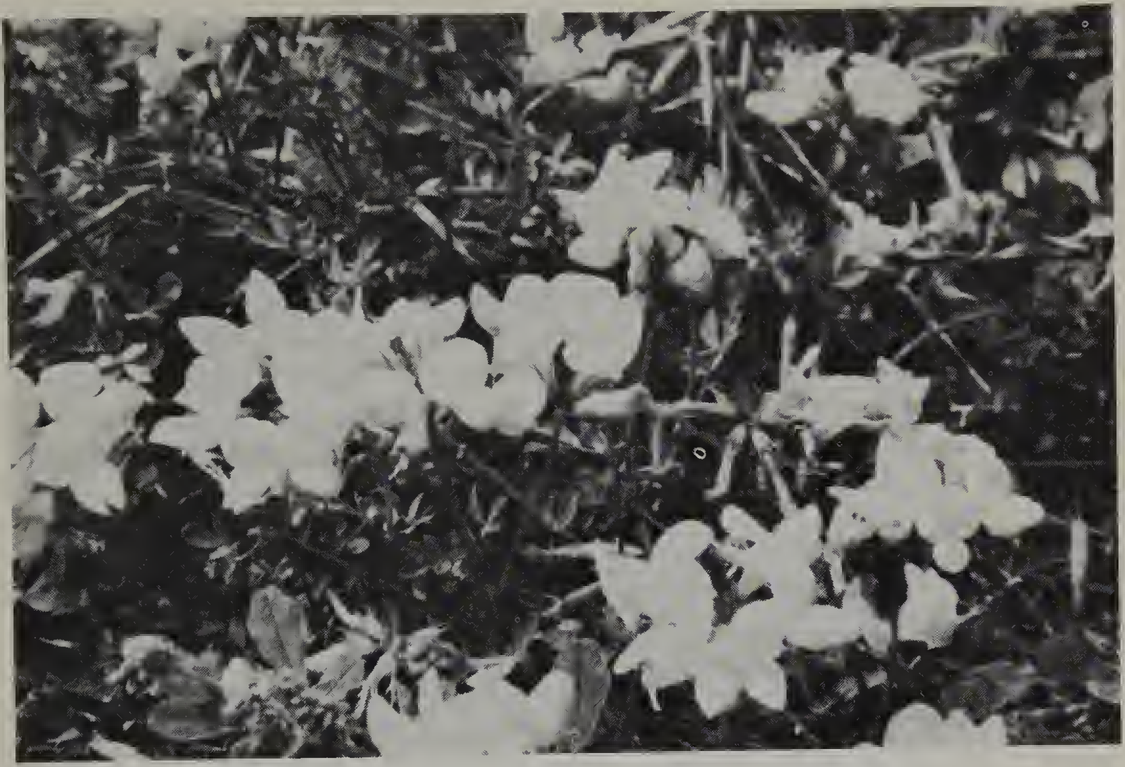


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Fig. 1-3 Bird's-foot trefoil, *Lotus corniculatus*, was found growing wild in eastern New York. An accidental import, it is now an important forage plant.

Physiological ecology depends upon experimental work under carefully controlled conditions. But the problems of forest management, range management, wildlife management, and other ecological fields still depend for their solution upon a broad ecological understanding of organisms in nature.

Field Biology and Taxonomy

Taxonomy is at the same time the oldest and the most basic of the biological sciences. For many years it was regarded by experimental biologists as a sterile and stagnant discipline, a study of endless and unimportant detail. The popular concept of the biologist as a rather musty character, tucked away in a corner surrounded by bottles, jars, and trays of specimens, or as a wild-eyed, unkempt man chasing insects off cliffs, net in hand, can be traced to the excesses of early taxonomists. Certainly the concept has little relationship to reality today. Intelligent classification of organisms may take into account such diverse fields as morphology, biochemistry, ethology, and ecology. Some taxonomists work exclusively with the study of chromosomes, some with biochemical assays, and others by comparing behavior patterns. Far from being stagnant, taxonomy is developing and changing very rapidly.

Part of the work of the taxonomist is, and no doubt will continue to be, brought about by the errors of the past. Some taxonomists who named species on the basis of specimens sent to them by collectors had little or no knowledge of the ecology of the animals and plants with which they dealt. Sometimes different names were applied to different stages of the same species, or to different color phases, or because of sexual or seasonal variations. For example, difference in size between males and females is particularly marked in American weasels (Fig. 1-4). Males may average 15 to 25 per cent longer and up to 50 per cent heavier than females. Since the several species show much size variation, taxonomists have concluded on several occasions that the two sexes of the same species represented different species or that the male of a smaller species and the female of a larger species were the same. Such mistakes are inevitable among early workers studying only a few specimens from scattered localities. These burdens of useless and confusing names form a continuing problem to the taxonomist (Hall, 1951).

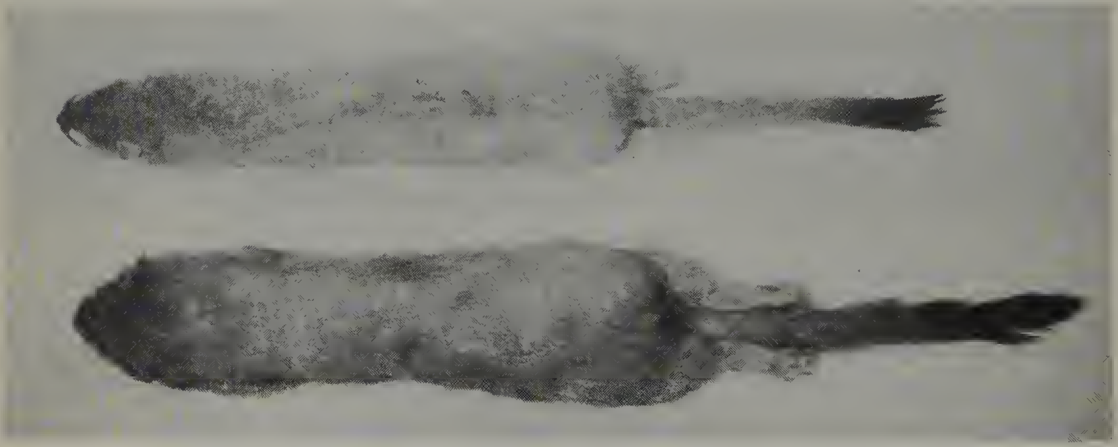

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Fig. 1-4 Male (bottom) and female of the long-tailed weasel, *Mustela frenata,* showing sexual difference in size.

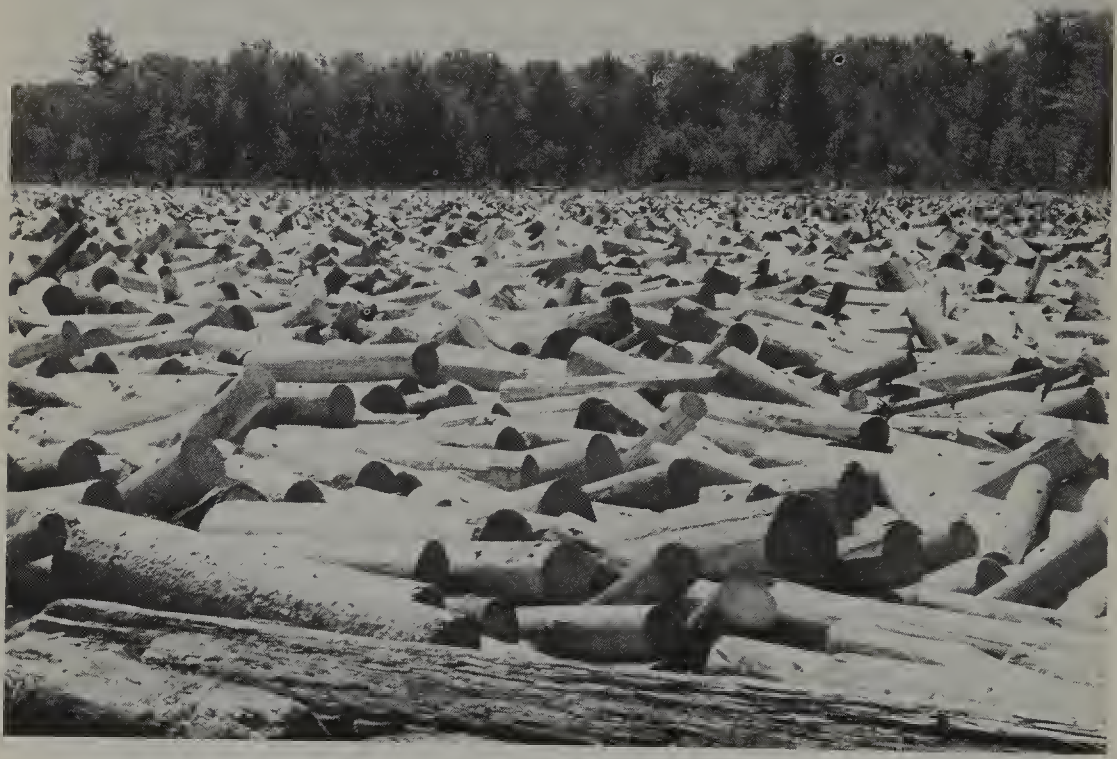
Modern taxonomic practice in most groups divides the species into smaller units called subspecies. While some biologists oppose such divisions (see p. 57), the practice has become widespread because it gives taxonomists a means of recording minor differences which may eventually be a part of species formation. In a sense, this is evolution in action at the population level. If two populations at the subspecific level become isolated from each other, they may diverge enough to become distinct species. Also significant is the fact that there are physiological and behavioral differences as well as purely morphological differences between subspecies. It may thus happen that studies of one subspecies are not entirely applicable to other forms of the same species.

In some groups, the subspecies concept has been abused. Some taxonomists have depended upon minor size differences or other insignificant characteristics to set up a multitude of "millimeter subspecies." Equally unfortunate has been the application of scientific names to abnormal individuals, or to minor seasonal variations. Some years ago, for example, a mole which was found on Anastasia Island off the coast of Florida was described as a new subspecies, *Scalopus aquaticus anastasae,* because of the golden color of its ventral surface. The validity of this form was finally brought into question by a field student of moles (Eadie, 1954), who pointed out that this golden color is a seasonal characteristic, apparently due to glandular activity, and has no taxonomic significance whatever.

Field Biology and Conservation

As world population increases and clamoring millions demand a higher standard of living than their ancestors knew, the problems of resource use take on added importance. The use of the world's resources for the greatest use of the greatest number for the greatest possible length of time has become an international problem of the utmost urgency. We are managing our environment as never before in history, and if we are to manage it wisely we must base our management on a sound foundation of ecological knowledge. Such knowledge must largely be gained by field study.

Our ancestors, in their understandable haste to clear the land and vanquish the wilderness, had little concern for careful use of natural resources. They had little knowledge of ecological processes, and if they thought about it at all they concluded that our resources were inexhaustible. This myth of inexhaustibility still clings to the American mind, while plants and animals pass into extinction, topsoil washes down our rivers, the water table continues to fall, and forests con-



Ralph S. Palmer

Fig. 1-5 Thousands of acres of trees must be harvested each year to supply our needs for hundreds of wood products. Forest conservation is thus a matter of growing concern to Americans.

tinue to perish before the ax and the saw (Fig. 1-5). With advancing land utilization, drainage of marshes, and a constant increase in the numbers of sportsmen, many of our native game species are in danger of extinction, following the dim trail of the Labrador duck and the passenger pigeon.

Again, the problems fall upon the shoulders of field biologists. Good land-use practices must be reconciled with good wildlife conservation practices. Game must be produced to satisfy the growing army of hunters—and that in the face of increasing destruction of wildlife habitat. Sportsmen must have more and better information if they are to accept protection of game as a necessity and not as unjust and unnecessary interference in their private affairs. Farmers must be convinced that game is a valuable crop, and that production of game is not incompatible with good agriculture.

The past half century has seen tremendous strides in knowledge of wildlife. Exhaustive studies have been made of some important species. Yet much work remains for the biologists employed by the conservation departments of the various states, by the U.S. Bureau of Sport Fisheries and Wildlife, and by private organizations. In many states, for example, bounties are still paid for the destruction of various species of unwanted wildlife. Competent field biologists are generally agreed that bounty money is wasted money (Latham, 1951) and that undesired species are not kept under control in this way. A few thousand dollars spent on habitat improvement or on removal of the undesired animals by a skilled field worker would do more good at less expense. In many cases, predator control is not needed and real harm to wildlife is done by unwise destruction of these animals. Dissemination of information as well as its acquisition is especially needed in this field of investigation.

Field Biology and Ethology

For half a century, the study of behavior in America was primarily a laboratory discipline and, indeed, was largely conducted by psychologists rather than by field workers. Study was for the most part confined to a few species: the pigeon, the rat, the domestic chicken, and a few primates. With the publication in 1936 of a paper by an Austrian scientist, Dr. Konrad Lorenz (see Chap. 10), the field biologist entered the realm of behavior study. Today the science of behavioral ecology is gradually developing (Klopfer, 1962), and the study of animal behavior is recognized as a proper branch of field biology. The laboratory conclusions of the past are being tested under natural conditions in the field (an interesting reversal of the usual order of things), and a whole new generation of ethologists is being produced in our colleges and universities.

Field Biology and Physiology

At first glance, the idea that field biology could have anything to offer to the study of physiology seems absurd. By the very nature of its operation, physiology has been restricted to laboratory work. Yet probably the fastest-developing branch of ecology today is physiological ecology. Several aspects of modern science have spurred this trend. Radiobiology, a field unknown thirty years ago, has led to the necessity of understanding the effects of radiation on organisms under natural environmental conditions. Transistorization of instruments has permitted greater portability, while newer and more sophisticated instruments are constantly produced by our instrumentation experts. Imaginative use of these instruments and the development of new techniques for field use have contributed to the rapid growth of this branch of ecology. From the viewpoint of today's world, it appears that the era of descriptive ecology has begun to give way to a new era of experimental ecology in which the physiologist will continue to play a leading part.

THE FIELD BIOLOGIST'S SKILLS

In order to make their contributions to human knowledge and welfare, the field biologists must possess certain skills and use certain techniques. A detailed discussion of these "tools of the trade" would occupy a book by itself (see Mosby, 1960). We may, however, consider briefly some of the indispensable items of intellectual equipment which the field biologist must have and see how they are used in the pursuit of his studies.

The Scientific Method

The scientist in any field is trained to reach his goal by a definite method of operation. It is hard to reduce this method to paper, but in simple form it may be thought of as a series of steps, as follows:

1. The Problem. A question or questions for which the answers are unknown. The formulation of the problem is often one of the most difficult steps in a study.
2. Accumulation of Facts (data). The literature is studied, field observations made, and questions asked.
3. Formulation of a Hypothesis. On the basis of the data, a suggested answer to the problem may appear.
4. Testing the Hypothesis. Experiments, observations, and continual checking of facts which may bear on the suggested answer.
5. Integration and Interpretation of Data. If the evidence supports the hypothesis, it may be possible to reach a conclusion. If data tend to disprove the hypothesis, we must return to Step 3 and start again. Some of the more basic hypotheses become "scientific laws" after they have been adequately tested.

Even the most unscientific reader will realize that not all —indeed, probably not even most—important scientific discoveries are made in exactly this manner. Luck may enter the picture, and the scientist may arrive at a conclusion without even asking the question. In a great many cases the answer to an entirely different question emerges during the progress of an investigation. Or one or another of the steps may be ignored as the scientist sees his way clearly. Nevertheless, this is a simple way to explain how scientists work, and why it is that the scientific work of one man may be repeated by another to check the results.

In field biology, this essential repeatability is less easy to guarantee than in the laboratory because it is difficult to control all the natural variables. Yet, the field biologist's aims are no different from those of his fellow scientists. Perhaps he leans more on observation and less on controlled experiments; perhaps he depends more upon probability and statistical analysis of data. But in the end his job is to discover the answers to problems about plants and animals in their natural habitat and to interpret these findings as they may be of importance to people. We may illustrate the ways in which field biologists work by examining a field study which followed the five steps of the scientific method rather closely and which produced some conclusions that were of significance in the relationships between people and wildlife.

In the early 1930s, a serious disease of elm trees was accidentally imported into the eastern United States from Holland. Caused by a fungus, *Ceratostomella ulmi,* this so-called Dutch elm disease was transmitted to native elms by beetles brought over in elm logs imported for making veneer. When these beetles emerge from pupation in a diseased tree, they carry with them spores and mycelia of the disease fungus. They fly to living trees nearby and feed on the outer branches, eating into the bark. When they penetrate the vascular tissue of the tree, the fungus invades the new tree, and the disease eventually kills the tree.

It seemed to early students of this disease that it might be easier to control the beetles than to stop the fungus itself. Efforts at control, therefore, were based on spraying healthy trees with the powerful and long-lasting insecticide, DDT, which killed the beetles before they could penetrate the vascular tissue of healthy elms (Fig. 1-6). Such spraying programs, however, always produced complaints about the killing of birds, fishes, and mammals in the sprayed areas.

The operators of the spray program and the owners of the

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Fig. 1-6 A DDT spray, applied twice during the spring and summer, was found to be effective in controlling the spread of Dutch elm disease.

trees were, of course, anxious to save the elms. Nonetheless, some concern was aroused by the destruction of birds and other wildlife. Should the spraying prove to be a case of large-scale death, the whole program would be endangered. A field biologist was therefore assigned to the job of evaluating the toll on wildlife caused by spraying in one locality where the program had been under way for several years.

1. *The Problem.* The specific problems faced by the biologist can be worded in these questions:

a. Does this spraying operation kill birds and other wildlife?

b. If so, is the kill of wildlife sufficient to outweigh the value of the elms saved?

c. Can means be devised to reduce or eliminate the loss of wildlife without losing the value of the spray program?

2. *Accumulation of Data.* DDT spray, in the concentration used in the program, had been shown in previous studies to be lethal to birds and mammals. Dead birds, mammals, and

fishes had been found in the sprayed area soon after spraying but had not been analyzed to discover the cause of death. The local people believed that DDT was causing a great number of casualties among the songbirds. No accurate count of animals killed was available, however, and the estimates of the landowners were so variable as to have little scientific value.

The spraying was done twice each year, once in April–May and again in July. Reports indicated that mortality had been higher after the spring spray, and careful questioning elicited the information that much of the mortality had occurred in areas which had been sprayed twice. Few field studies of DDT-sprayed areas had been made at this time, but in view of the known toxicity of DDT it seemed reasonable to assume that at least part of the observed mortality was due to DDT poisoning.

3. *Formulation of a Hypothesis.* With the accumulated data at hand, certain hypotheses could be stated:

a. DDT was responsible for some mortality of local wildlife, particularly insectivorous birds.

b. The effect was most marked after spring spraying.

c. Areas receiving heavy concentrations of spray because of the large number of elms or because of accidental double doses of spray were most seriously affected.

4. *Testing the Hypothesis.* In order to test these hypotheses in a scientific manner and to secure additional data which might shed some light on the problem, the biologist selected a study area in the midst of a section of high elm population which had been sprayed regularly for several years. A check area of similar vegetation was chosen outside the sprayed area, but near enough so that the bird population could be expected to be similar. Studies of the bird populations of these two areas were made by standard bird-census methods, both before and after the summer spraying. Bird nests were studied in both areas to determine nestling mortality. Dead birds and mammals were collected from both areas and analyzed for the presence of DDT derivatives in the tissues. The observer studied the behavior of birds on both plots to find out whether the spraying had any effect upon behavior. The program of study was carried over into the following spring, so as to evaluate the results of both sprayings.

5. *Interpretation of Data.* After the studies were completed, the investigator had a wealth of data. He had to examine and synthesize the results of some 50 daily censuses of birds in the two areas. He compared nestling mortality in the two areas to determine if it was markedly higher in the sprayed area. He received and analyzed reports on the autopsies of dozens of dead birds. He studied the dates of maximum mortality in relation to the spraying program. He received and checked out numerous reports of sick or dead birds discovered by local people.

These data permitted him to reach definite conclusions with regard to the original questions and to make some recommendations which might improve the situation from the wildlife viewpoint. The data substantially supported the hypotheses stated in Step 3 and gave rise to the following conclusions:

a. Chemical analyses of the carcasses of dead birds and mammals indicated that DDT was the cause of considerable mortality.

b. Mortality was higher during spring, when large numbers of migratory birds were in the area.

c. Mortality was light or lacking in areas where elms were few, but heavy in areas with extensive plantings of elms.

d. Most of the birds killed in summer were young and nestling birds.

e. Adult populations were not significantly smaller after the summer spraying than before.

f. Most of the spring mortality occurred in late April and May, during the peak of migration, and involved migratory species in greater numbers than resident species.

From these conclusions, the investigator made the following recommendations:

a. Spraying should be kept to the minimum necessary for adequate beetle control.

b. Spring spraying should be completed as early as weather would permit, to avoid the peak of migration.

c. Summer spraying should be delayed until the peak of the nesting season was past to avoid excessive mortality among nestlings.

d. Mortality among vertebrates other than birds was not noticeably important during the period of study and did not appear to be a serious hazard in the area under consideration. However, in view of the known cumulative effect of DDT derivatives, the possibility of future losses could not be ignored.

At the end of the study, evidence was not available to indicate whether these measures would be effective in reducing bird mortality. It did, however, produce data which could bring about immediate adjustments in the procedure of spraying (Blagbrough, 1952).

You will note that the investigator in this project utilized a variety of field techniques which are of broad application in ecological problems. They may be summarized as follows:

1. Formulation of experimental procedure; selection of comparable areas for study
2. Census procedures (particularly birds in this case)
3. Identification of plants and animals
4. Study of bird behavior; location of bird nests; preservation of specimens for future study
5. Field study of ecological distribution, daily activity, feeding, etc., with particular reference to birds
6. Analysis of data to determine significance of variations in populations and other numerically determinable items

These techniques and similar ones concerned with other groups of organisms are so generally useful in field research that they may apply to almost any problem of ecology. They require the ability to recognize certain species in the field, a knowledge and understanding of normal behavior and habits of organisms, the ability to use standard ecological techniques and instruments, and the ability to formulate a problem and analyze data. Modern field biology may also require the use of electronic instruments, radioactive materials, advanced statistical methods, and other tools and techniques, which are being developed and refined each year. Some of the more important of these are discussed in the Appendix, and others in the books listed at the end of this chapter.

The field biologist, then, depends for his success as a research worker upon a broad spectrum of materials and knowledge. As for method, the field biologist might well take for his slogan the one which hung on the wall of the laboratory used by the famous Russian physiologist Pavlov: "Observation, and again observation."

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chapter 2

A brief history of field biology in America

Field biology has always been an important aspect of American cultural and intellectual life. Some of our most illustrious men have contributed to its development, and its course has had a profound effect on the history of our country. In a single chapter, it will be possible to follow only the main stream of accomplishment, with occasional brief excursions into some of the more interesting side branches. In general, we shall attempt to trace the development of ideas and movements, but in so doing it will be necessary to discuss the men who gave birth to the ideas and gave direction to the movements. Although much that is important has occurred in the past half century, we shall, for the sake of perspective, end our survey with the beginning of the 1900s, so as to include the formation and early years of several great movements which had their origin around the turn of the century.

THE COLONIAL PERIOD

The years of colonization and expansion, from 1607 to 1775, saw the laying of the cornerstone of American field

It is the exclusive property of man, to contemplate and to reason on the great book of nature. She gradually unfolds herself to him, who with patience and perseverance, will search into her mysteries; and when the memory of the present and of past generations shall be obliterated, he shall enjoy the high privilege of living in the minds of his successors, as he has been advanced in the dignity of his nature, by the labours of those who went before him.

Carolus Linnaeus, "Species Plantarum"

biology. The workers of those early days were scattered, in both space and time, and for the most part worked independently. These pioneer collectors and observers were in many cases only passing visitors to our shores, such as Peter Kalm, the Swedish botanist. Others, however, stayed for longer periods or were indigenous naturalists who spent their entire lives in America. It is with this latter group that we shall mainly concern ourselves.

The seventeenth-century American had little time or interest for the study of nature on the new continent. Some early travelers, like the redoubtable John Smith of Virginia, wrote books about their travels, in which they described some of the most interesting plants and animals, often with fanciful additions. The first biologist to do any work of significance in the colonies, however, was Thomas Harriot (1560–1621). Harriot was a friend of Sir Walter Raleigh, with whom he came to America in 1585. In "A Briefe and True Report of the New Found Land of Virginia," published in 1590, he described more than a hundred animals and many plants.

Other students of nature followed in small numbers through the seventeenth century. In 1637, King Charles I dispatched a young man named John Tradescant to collect plants and shells in Virginia. Tradescant's father was a botanist, and the surname is commemorated in the generic name of the spiderworts, *Tradescantia.* A few years later, in the 1660s, John Bannister, a friend of the English biologist John Ray, came to Virginia and collected biological materials. His paper on the plants of Virginia, published in 1686, was probably the first taxonomic paper produced in America. Bannister, a young man of great promise, was killed on a plant-collecting expedition when he fell among the rocks at the falls of the Roanoke.

In New England, a few semiscientific works on biology were published during the seventeenth century. William Wood's "New England Prospect" and Thomas Morton's "New England Canaan" were more literary than scientific. At a somewhat higher level of biological accuracy were John Josselyn's "New England's Rarities" (1672) and "Account of Two Voyages to New England" (1675). The century ended, however, with little important knowledge of American plants and animals having been published.

The pioneers, whether hunters, trappers, or farmers, were vitally interested in the wild animals and vegetation which they had to conquer, but few of them were able to write, and even fewer cared to record the knowledge which they had accumulated. Until there was time for a cultured and leisurely class to develop, observations on nature were made available only through travel books or the occasional notes in the journal of a missionary, doctor, or other educated person.

The beginning of the eighteenth century, however, saw the influx into America of many Europeans of scientific bent. Some came to settle, but others came for the express purpose of discovering and collecting the rich natural wonders of America. To Virginia, about 1700, came John Mitchell, a biologist of some ability. He remained in Virginia until 1746, when he returned to England. His most important work was his "Dissertation upon the Elements of Botany and Zoology" (1738), but he also contributed specimens to European taxonomists. The beautiful little partridgeberry, *Mitchella repens*, bears his name.

John Clayton

Close upon Mitchell's heels came John Clayton (1685–1773), a botanist, who arrived in Virginia in 1705 to serve as a clerk. He worked long and faithfully in this capacity, and in his spare time collected plants and seeds for transmission to friends and acquaintances in Europe. As the years passed he became well known, and by mid-century he was corresponding with Linnaeus and other European biologists. The great "Flora Virginica" of Gronovius, published in 1739–1743, was based largely on the work of Clayton. The second edition, having a publication date of 1762, after the Linnaean system was established, is the basis of many botanical names which still stand. Clayton is remembered in the generic name of the spring beauty, *Claytonia,* named for him by his friend and co-worker, Gronovius. Before his death in 1773, Clayton became a correspondent of Benjamin Franklin, Thomas Jefferson, and most of the other prominent scientists of his day. His manuscripts and specimens, unfortunately, were destroyed by fire during the Revolutionary War.

Cadwallader Colden

In 1710, Cadwallader Colden (1688–1776) arrived in Philadelphia from Europe. He had studied medicine in London and came to the New World to begin his career as a doctor. Being of a friendly and prepossessing personality, he became intimate with important New York politicians, and in 1718 moved there in expectation of a political appointment. This he received in 1720, when he became surveyor general of the colony. He spent the rest of his life in public service, and in his spare time wrote numerous treatises on botany, medicine, mathematics, and philosophy. Colden's most important biological work was an extensive paper dealing with new American plants, which Linnaeus published in Sweden in 1749. Colden's daughter, Jane, was also a capable botanist.

Mark Catesby

In 1712 one of the great figures of American natural history landed in Virginia for a visit. He was Mark Catesby (1679–1749), who had studied natural history in England, and who immediately succumbed to the fascination of the New World. In 1719 he returned to England to secure financial backing for a natural history survey of the Southeast. He was successful in securing money, and in 1722 he was back in this country in what is now South Carolina. For four years he studied and collected in the Southeast and in the Bahamas. In 1726 he returned to England to write a report on his collections. This "Natural History of Carolina, Florida and the Bahama Islands" was published in three parts from 1731 to 1748. Before his death, Catesby was recognized for his pioneer work by election to the Royal Society. Since his publications appeared before the work of Linnaeus, few of his scientific names of organisms are still in use today; but he is commemorated in the scientific name of the bullfrog, which Linnaeus named *Rana catesbiana* in his honor.

Many European travelers capitalized on their experiences by writing books upon their return to Europe. Much of our information about the status of American wildlife and plants at that time has been gleaned from the works of such travelers as Kalm,* Anbury,† Lahontan,‡ and Campbell.§ Other visitors made somewhat longer stays and contributed markedly to our knowledge of the flora and fauna. Outstanding among these were André Michaux and his son François, who together laid the foundation for American forestry. François's book on North American trees remains one of the great classics of botany.

In Charleston, South Carolina, Dr. Alexander Garden collected all manner of biological specimens from 1750 until the Revolutionary War. After the war he returned to England, but his biological career is commemorated in the name *Gardenia,* familiar to all lovers of flowers.

The Bartrams

Meanwhile, a completely untutored biologist was beginning a life work which would have a tremendous and permanent effect on American field biology. John Bartram (1699–1777) was described by classifier Carolus Linnaeus as "the greatest natural botanist in the world." Bartram was also interested in every other phase of natural history. A Quaker farmer, he became so obsessed with nature that he risked his life on travels to collect natural objects for European biologists and curio seekers. In 1728 he established a horticultural garden near Philadelphia, to which he brought all the new plants found in his travels. Through correspondence with the English botanist Peter Collinson, he was brought into contact with Linnaeus in Sweden, Gronovius in Holland, and other important European biologists. He corresponded extensively with Clayton and Colden, and was acquainted with Benjamin Franklin and George Washington. His garden on the Schuylkill River was a popular haunt of the scientifically inclined intellectuals of Philadelphia, and his influence may well have been important in the founding of the Academy of Natural Sciences of Philadelphia some thirty-five years after his death.

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* Kalm, Peter. 1770–1771. "Travels into North America." Trans. from Swedish by J. R. Forster. 2 vols. vol. 1, 414 pp.; vol. 2, 423 pp. London.

† Anbury, Thomas. 1789. "Travels through the Interior Part of America, in a Series of Letters." vol. 1. London.

‡ Lahontan, Louis Armand deLom D'Arce. 1703. "Some New Voyages to North America." London.

§ Campbell, P. 1793. "Travels in the Interior Inhabited Parts of North America in the Years 1791 and 1792." Edinburgh.

William Bartram (Fig. 2-1) was the only one of John Bartram's children to follow in his father's footsteps. He started his adult life as a trader but soon returned to his first

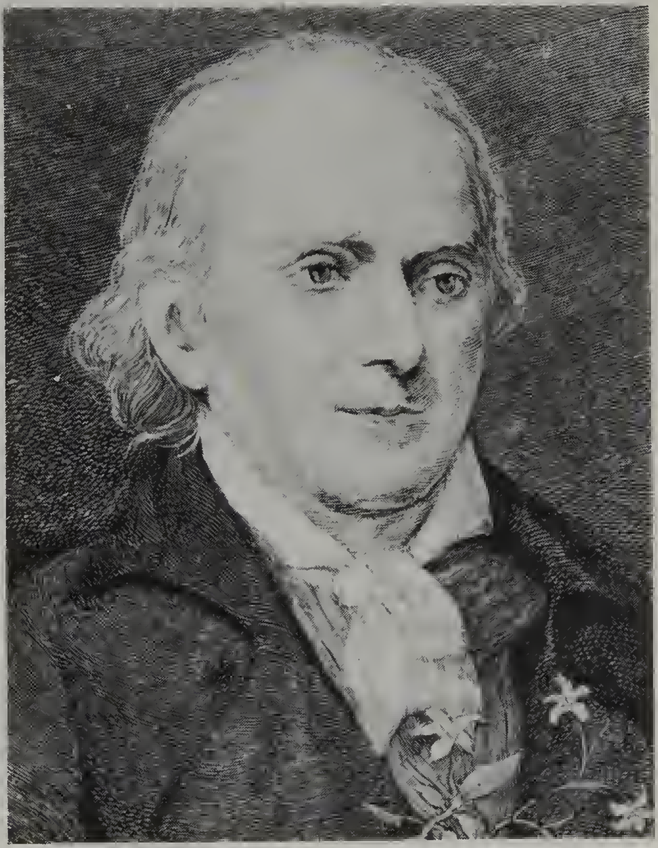

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Fig. 2-1 William Bartram, 1739–1923.

love—exploring, collecting, and drawing natural objects. In 1791 he published an account of his travels in the Southern states. This book met with great acclaim in Europe, was translated into several languages, and brought Bartram before the eyes of the European biologists. A fine ornithologist as well as a botanist, he was of assistance to Alexander Wilson in his work on American birds. In honor of his friend, Wilson named the upland plover *Bartramia longicauda.*

Early Scientific Societies

By the beginning of the nineteenth century, exploratory work in the Eastern states was well under way. The number of active workers was increasing, although it was still pitifully small. Nonetheless, learned societies began to spring up in cultural centers, and these societies attracted new workers into the field. The first of these groups was the American Philosophical Society, organized in 1743 at Philadelphia. Since its early years under the aegis of such notable presidents as Benjamin Franklin and Thomas Jefferson, it has had steady growth and increasing influence. In 1812, the Academy of Natural Sciences of Philadelphia was formed. Led by such able men as Thomas Say, Thomas Nuttall, and Gerard Troost, it became, and remains today, an active force in the study of natural history. In 1817, the Lyceum of Natural History of New York was founded, and this organization still exists as the New York Academy of Sciences. Boston followed in 1830 with the formation of the Boston Society of Natural History.

THE ERA OF AUDUBON

Although the few learned societies of the early nineteenth century did much to advance the study of science, American field biology in this period was advanced largely by a group of the most ill-assorted and eccentric geniuses probably ever assembled in a single country at one time. Most of them came from abroad: a gay French dancing master turned trader; an eccentric cosmopolite of French ancestry, born in Turkey, and trained in Sicily; a poor Scottish weaver and poet, out to make his fortune in the new world. Among them, they scanned the whole field of natural history, and their contributions to science were so vast as to be almost unbelievable in this age of specialization. In those frontier days they ranged from the east coast to the Mississippi, and occasionally joined expeditions to the

Rockies or the west coast, collecting, observing, describing as they went. Three of these great naturalists, each of whom followed his own genius wherever it led him, seem to group naturally together.

John James Audubon

Certainly the best known of the towering figures in the field of natural history in that era was John James Audubon (Fig. 2-2.). Born in 1785, the illegitimate son of a French sea captain and a Creole of Santo Domingo, he was legally adopted by his father and educated in France. In 1803 he was sent to America to work on his father's plantation in Pennsylvania. Much more interested in dancing, drawing, music, and sport than in the work of the plantation, he cut a dashing figure in the drawing rooms of the local aristocracy. When it became evident that he was not much of a plantation manager, he joined in a trading venture on the frontier in Kentucky. He

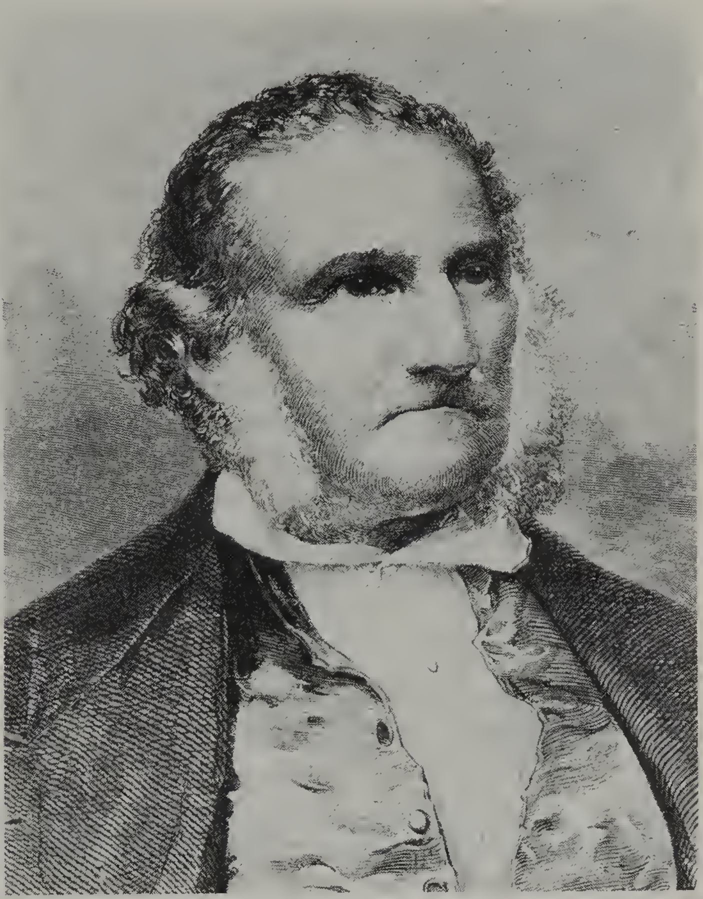

Fig. 2-2 John James Audubon, 1785–1851.

took with him his young wife, Lucy Bakewell Audubon, who was to be the balance wheel of his existence for many difficult years. Audubon preferred to spend his time collecting and drawing birds rather than tending his store, and bankruptcy followed wherever he went. Apparently he had no intention of capitalizing on his interests and talents until a chance meeting with Alexander Wilson, who was preparing his great work on American birds, crystallized Audubon's ideas and set him to work on a similar project. He began to travel widely, while his wife supported the family by teaching here and there. In 1823, Audubon felt that his work was ready for publication, but no American publisher would handle it. Undiscouraged, he sailed for England to find a sponsor there. An exhibition of his paintings in London met with overwhelming success. In a matter of days he secured a publisher and engraver as well as a host of influential friends. After a trip to France, he returned to America as a sort of public hero and elder statesman among naturalists. Always quite confident of his abilities and prospects, he was not noticeably affected by public adulation. He continued to work at his painting and writing; before his death he completed his "Ornithological Biography," which consisted of life-history studies of North American birds, and the paintings for "The Quadrupeds of North America," for which John Bachman did the text.

Alexander Wilson

The other giant of American ornithology was Audubon's opposite in many ways. Alexander Wilson (1776–1813) was born in Scotland to poor parents who apprenticed him to a weaver. A sensitive and poetic person by nature, Wilson was outraged by the treatment of the laborers of his day. His satirical lampoons of local industrialists caused him to be *persona non grata* in his own town, and he decided to try his luck in America. Although his education was largely self-administered, he succeeded in getting employment as a teacher, and eventually found his way to a school near the Bartram plantation at Philadelphia. Upon discovering Wilson's absorbed interest in birds, William Bartram and others of his circle persuaded Wilson to embark upon an ambitious project —nothing less than a monograph on North American ornithology. For a person without money, without literary or artistic training, and with no background whatever in scientific study, this might seem like a foolhardy venture; and so it appeared to most of the people who Wilson hoped would contribute to the support of such a study. Nonetheless, Wilson persevered, and succeeded in selling enough subscriptions to his work to be able to begin publication in 1809. It was a monumental opus in nine volumes, but Wilson did not live to enjoy the fruits of his labors. He died in Philadelphia in 1813 before the last volumes of his life work appeared.

C. S. Rafinesque

While the birds were absorbing the attention of Audubon and Wilson, the rest of the biological world was not being neglected. One man, a genius of tremendous proportions, encompassed the whole field of biology (and many other fields as well), and threw away most of the results of his genius by careless work and personal eccentricities. Constantine Samuel Rafinesque-Schmaltz (1783–1840) was born of French and German parents in Turkey. Soon thereafter, his family moved to Italy, where young Constantine became interested in natural history and published his first work on botany. In 1802, after the death of his father, he came to America and soon fell in with the Philadelphia naturalists, who had much influence on the direction of field biology in America. Because of his extensive knowledge of botany, Rafinesque hoped to secure the position of botanist for the Lewis and Clark Expedition, but failing to do so, he returned to Italy in 1805. Here he married, and two children were born. His son died at an early age, and a few years later his wife ran away with a traveling entertainer, taking their daughter with her. Rafinesque, heartbroken and embittered, gathered together his extensive notes and journals on American and European natural history, packed up his collections, and embarked again for America. Off Long Island his ship was wrecked and all his notes and collections were destroyed; Rafinesque was fortunate to escape with his life.

With this background it is perhaps a little easier to understand Rafinesque's later career. For several years he wandered over the United States, tutoring here and there, meeting other biologists, professional and amateur, and collecting and describing plants, fishes, mammals, insects, mollusks, and practically everything which came to his attention. In 1819 he was enabled, through a friend, to obtain the post of professor of natural history at Transylvania University, in Lexington, Kentucky. He was a popular and talented teacher, but his talents did not extend to getting along with others. Although these were the most productive years of his life, he antagonized many of his colleagues by careless work, descriptions based on hearsay, and attacks on the ability and character of those whom he disliked. In 1825, the president of Transylvania University dismissed him from his position, and Rafinesque again set out on his wanderings. After visiting other biologists and teachers, such as Amos Eaton at Troy, New York, John Torrey in New York City, and his old friends at Philadelphia, Rafinesque settled down in Philadelphia to attempt to make a living. An abortive banking scheme kept him in funds for a time. An offer of money for collecting materials for Cuvier in France was withdrawn when Cuvier died. Worn out by cancer, embittered by his misfortune, Rafinesque died in 1840, and only the vigilance of a friend saved his body from being sold to a medical school to pay for his back rent.

A number of other persons with an interest in natural history worked in the United States during this period. Manasseh Cutler (1745–1823) was the first to publish a systematic account of the plants of New England. A Congregational minister, Cutler was also a lawyer, physician, and scientist, and one of the early followers of the Linnaean system. In Pennsylvania another minister, Gotthilf Muhlenberg, published a catalogue of North American plants in 1813, listing 2,800 species. A genus of grasses, *Muhlenbergia*, is one of several scientific memorials of his name. Still another cleric, John Bachman, collaborated with Audubon in their great monograph "The Quadrupeds of North America" and was competent in other fields of natural history as well.

THE NEW HARMONY MOVEMENT

A very large proportion of the biologists of the early part of the nineteenth century were affected in one way or another by a remarkable social experiment which was carried on at this time. In 1824, Robert Owen, an English industrialist with a remarkable social conscience for one of his generation, purchased the village of Harmonie, Indiana, from the Rappites, a religious sect that was establishing a new community farther up the Ohio River. Here Owen planned to organize the world's first scientific community, which he called New Harmony. His plan was to gather one or two thousand people who wished to take part in his social experiment which promised security, culture, and an easy life in return for giving up family life and personal property.

Owen chose William Maclure, a geologist from Philadelphia, as director of education for New Harmony, and Maclure enthusiastically began to gather suitable personnel for his "university." The group sailed from Philadelphia to New Harmony in a small keelboat satirically dubbed the "Boat-load of Knowledge." Among the notables involved in this journey, two were field biologists of great ability.

Thomas Say

Thomas Say (1787–1834) had nearly the genius of Rafinesque but none of Rafinesque's eccentricity. The son of a physician, and great-grandson of John Bartram, he was fascinated by plants and animals from early youth. At the age of fifteen, unable to see any future in science, he took up an apprenticeship in his father's apothecary shop.

For some years Say and a few friends of similar scientific bent met occasionally at the shop of another apothecary, John Speakman, to discuss natural history. In 1812, Speakman suggested that they form a scientific society and have regular meetings. This proposal met with general favor and resulted in the formation of the Academy of Natural Sciences of Philadelphia. Say, who by now was in charge of the apothecary shop, gave so much time to the new Academy that his business went rapidly downhill and eventually failed. Say, no doubt with a sigh of relief at having been so easily relieved of his burdens, moved into the Academy museum and began to spend all his time in the pursuit of his studies.

In 1817, Say published a part of what was to have been a complete survey of North American insects. Before it was finished, however, he had taken up the study of mollusks and was well versed in other fields of natural history, so that this first great work remained incomplete. His extensive knowledge led to his employment, in 1819, as geologist with the Long expedition to the Rocky Mountains. The expedition traveled over much of the prairie between the Mississippi and the foothills of the Rockies, collecting hundreds of unknown species. As a well-known zoologist, Say was appointed, in 1822, to the chair of Natural History at the University of Pennsylvania. Here he remained until 1825, when his friend Maclure persuaded him to take part in the New Harmony movement as superintendent of literature. He retained this position until his death in 1834, producing voluminous works on insects and mollusks. It is said that Say described more species of animals than have been described by any other single American biologist.

Charles LeSueur

Charles Alexander LeSueur (1776–1846) was a French artist who became interested in natural history while on an expedition to Australia. In 1815 he came to America with William Maclure and settled in Philadelphia. His interest in science led him to the Academy of Natural Sciences, where he served as curator while teaching art for a living. After joining the New Harmony movement in 1825, he made numerous trips to the Mississippi Valley and the Southeast, specializing in the study of fishes. His studies and descriptions laid the groundwork for American ichthyology, and with that of Rafinesque, his work resulted in the discovery of most of the species of eastern fishes. When the New Harmony experiment failed, after Say's death, LeSueur returned to France, where he died in 1846.

Many other scientists visited and worked at New Harmony during its brief existence. Rafinesque visited there from time to time, and European visitors like Charles Lyell and Prince Maximilian du Weid stopped by in the course of their travels. With the demise of New Harmony, there developed in American biology a vacuum which had no immediate prospect of being filled.

PIONEER BIOLOGY TEACHERS

Biology, however, had for some time been assuming an air of intellectual respectability by being taught in American colleges. In 1768 a course in botany was given at the College of Philadelphia, by Adam Kuhn, and the course was continued under William Bartram in 1782. The first natural history course in this country was given at Harvard by Dr. Benjamin Waterhouse, starting in 1788. Waterhouse was soon joined in the field of biology teaching by Benjamin S. Barton (Fig. 2-3) at the College of Philadelphia in 1789, Samuel L. Mitchill at Columbia University in 1792, and Thomas Cooper at Dickinson College in 1811. In most cases, these early teachers were chemists, physicists, geologists, or physicians, who were given the chair of natural history because they had the closest

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Fig. 2-3 Benjamin S. Barton, 1766–1815.

approach to biological training which was available at that time. Waterhouse was joined at Harvard in 1805 by William Peck, a zoologist of great promise. Peck, however, died in 1823, and was succeeded by Thomas Nuttall, who was appointed curator of botany. Nuttall was of a retiring nature and did not enjoy teaching, so he remained at Harvard for only a few years, after which he resigned to travel and study. Those who have read Richard Henry Dana's classic sea adventure, "Two Years before the Mast," may recall that the ship on which Dana was a sailor picked up Thomas Nuttall at Monterey, California, and gave him transportation back around the Horn to Boston. Nuttall's place at Harvard remained vacant for some years, although lectures in natural history were given in the meantime by T. W. Harris, a physician, librarian, and amateur entomologist. Meanwhile, Nuttall became famous for his treatises on botany and ornithology, before returning to England to live on the family estate which he had inherited.

In 1842, the professorship of natural history at Harvard was given to Asa Gray, whose works on botany had already placed him in the front rank of American scientists. During this same period Amos Eaton had given a series of lectures on natural history at Amherst College and had opened a school at

Troy, New York, the forerunner of Rensselaer Polytechnic Institute, where he taught geology, chemistry, and natural history. Besides his classroom teaching, Eaton was a popular lecturer and tutored many interested amateurs in the sciences.

At Dickinson College in Pennsylvania, Spencer Fullerton Baird was employed to teach natural history, starting in 1846. Baird was the first to introduce field study of natural history into the American college curriculum, although he was only a short step ahead of another famous biologist who had already done much the same sort of thing in Europe.

Louis Agassiz

This European pioneer in biology teaching was Louis Agassiz (Fig. 2-4) (1807–1873) who, after receiving degrees from several universities in his native Switzerland and elsewhere in Europe and writing several monographs on geology and natural history, came to Boston in 1846 to deliver a series

Fig. 2-4 Louis Agassiz, 1807–1873.

of lectures. A noted authority and a fine lecturer, he soon became a famous figure in the intellectual circles of New England. In 1848, he accepted the position of professor of natural history at Harvard, and soon became the leading American proponent of natural history. Students flocked to his classes, and his students and associates soon spread his knowledge and his methods over the entire country. His famous dictum, "Study nature, not books," has been the rallying cry of naturalists ever since. He did not hesitate, however, to produce books for people to study. Among his works are four volumes of a proposed ten-volume work on the natural history of the United States, which was never finished. He founded the first American biological station at Penikese Island, and undoubtedly had more influence on American biological thought and teaching in the last century than any other single person.

GOVERNMENT BIOLOGISTS

At about the time Agassiz came to America, a new trend in biology appeared—the entrance of government into biological research. In 1841, T. W. Harris wrote a "Report on Insects Injurious to Vegetation," the cost of which was partly defrayed by the state of Massachusetts. In New York, under the influence of Amos Eaton and other scientists, a series on the natural history of New York was published, with five volumes on zoology by James DeKay and two on botany by John Torrey (Fig. 2-5), as well as others on geology, mineralogy, and agriculture. Although George Washington, in his annual message to Congress for 1796, had requested funds for the establishment of a national board of agriculture, it was not until 1853 that such a bureau was formed within the framework of the U.S. Patent Office. In 1846 the Smithsonian Institution was established in Washington under government supervision, and in 1850 Spencer Fullerton Baird was employed as assistant secretary. Under his leadership, the museum there soon became the best in the entire country. In 1871 a national Fish Commission was formed, with Baird as its head. In connection with this work, Baird founded the marine biological station at Woods Hole, Massachusetts, which remains an important education and research center to the present time. Baird was a prodigious worker with a passion for accuracy, and his monumental works on mammals, birds, reptiles, and fishes are still used by biologists.

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Fig. 2-5 John Torrey, 1796–1873.

In spite of the study of insects by Say and other workers, little official notice had been taken of entomology. In the 1870s, however, an outbreak of migratory locusts brought about the establishment of a national Entomological Commission. C. V. Riley was the head of this commission, and continued active in this work until his death in 1895. By that time the Commission had advanced to a Division of Entomology in the Department of Agriculture, doing extensive field work all over the country.

These pioneer workers in governmental biology were so successful that in a short time state entomologists, botanists, and zoologists began to appear all over the country. In 1878, the states of New Hampshire and California formed state game commissions, and similar organizations soon appeared in other states. Meanwhile, the United States Fish Commission had been formed, and a forestry agent, Franklin Hough, had been appointed in the Department of Agriculture in 1876. The trend continued with the establishment of a Division of Economic Ornithology and Mammalogy in the Department of Agriculture in 1885. This division later became the Bureau of Biological Survey, which was combined with the Bureau of Fisheries in 1940 to become the present Fish and Wildlife Service. State experimental stations began with one in Connecticut in 1875, and the idea soon spread to other states.

THE RISE OF POPULAR NATURAL HISTORY

Meanwhile the work of colleges and private individuals continued to progress. Colleges staffed by the students of Louis Agassiz, or by like-minded biologists, began to teach more and better biology. The emergence of the theory of evolution in England gave impetus to biological study, both among the proponents and opponents of the theory. Manuals of biology for the use of amateurs began to appear, though most were too technical for the ordinary layman. David Starr Jordan published his “Manual of the Vertebrate Animals” in 1876, while Asa Gray’s “Manual of Botany” and Elliott Coues’s “Key to North American Birds” appeared earlier. Edward Drinker Cope and Spencer Fullerton Baird had laid the foundation for further study of reptiles, amphibians, mammals, and fishes. Monographs of most of the great natural groups of plants and animals had been completed. With the completion of the transcontinental railroad, almost every corner of the country had been explored, at least cursorily. Biology had become a field so vast and compartmentalized that the old days of the untrained naturalist were gone forever. The naturalist, in the sense in which the term is often used, had lost his place in professional biology. The closest approach to the old natural history was the field work of the U.S. Biological Survey (later the U.S. Fish and Wildlife Service) with such scientists as C. Hart Merriam (author of the life-zone theory), Vernon Bailey, and Bailey’s talented wife, Merriam’s sister Florence. Naturalists in the armed forces, such as Elliott Coues and Edgar Mearns, studied nature in the far places to which their duty took them.

Biology in many colleges was confined to the laboratory, where great challenges confronted the student of comparative anatomy, embryology, genetics, and evolution. Field biology had become temporarily a sort of stepchild of science, with undoubted economic significance and some public appeal, but the great days of natural history seemed to have passed.

THE NEW ERA OF FIELD BIOLOGY

In the last quarter of the nineteenth century, several great movements were born which were destined to bring about the rise of field biology, amateur and professional, to a new peak of popularity and importance. With a brief review of the early development of each of these movements, we must end our glance at the background of field biology.

The Conservation Movement

Americans have been brought up, since the settlement of the colonies, to regard nature as something that must be conquered. Forests were to be eliminated to make way for farms; wild animals to be destroyed if they stood in the way of progress; land to be exploited for what could be wrung from it, and then abandoned for the land over the next mountain. We ought not to blame the pioneers for the immense energy with which they compassed this destruction, for it was a product of the times and the circumstances. People believed the myth that resources are inexhaustible, believed that there will always be more land, more forests, more wildlife, and more minerals.

With the later years of the nineteenth century, this myth was rudely shattered. The last mountain had been crossed, the last great forests felt the bite of the ax, the last individual of several species of wildlife had fallen before the fowler's gun or perished in the lonely confinement of a zoo. It was evident to professional men such as Franklin Hough and Gifford Pinchot that our forests were on the verge of complete destruction. The members of the newly formed American Ornithologists' Union were uncomfortably aware that the passenger pigeon and Labrador duck had passed beyond recall and that many other game birds and mammals might soon follow them down the road to oblivion. Families which had moved successively from New England to New York to the Midwest to the Pacific coast found that there was no further frontier. It was obvious to the lovers of nature that the time had come to "gather at Armageddon and battle for the Lord."

Soon after 1900 the Audubon Society, led by Frank Chapman and others, was engaged in a fierce battle with the despoilers of wildlife, to protect endangered species of birds, such as the egrets, from complete extinction. Foresters like Bernhard Fernow, Gifford Pinchot, and Henry Graves were urging the "long look ahead" and sustained-yield forestry. A few men who were in position to realize the problem were fighting the abuses involved in giving away the public domain, those millions of acres of public land distributed under the Homestead Act of 1862, the Timber and Stone Act of 1878, and other related legislation. The friends of conservation had succeeded in getting through Congress, in 1891, a bill to permit creation of forest reserves within the nationally owned forests. A commission appointed by Grover Cleveland in 1896 had examined the nation's forest resources and made recommendations on handling them, but Cleveland, a firm supporter of conservation measures, left office the next year, with most of the nation's resources still in danger.

The turn of the century saw a change in the affairs of conservation. In 1901, Theodore Roosevelt, an outdoorsman, hunter, and competent field biologist as well as politician, became President of the United States. In Gifford Pinchot, forester in the Department of Agriculture, C. Hart Merriam, and T. S. Palmer of the Biological Survey, and congressmen like John Lacey of Iowa, he had strong allies within the government. Conservation acts, one after another, began to pass into the law books. Acts forbidding the feather traffic, acts setting aside or authorizing the setting aside of vast areas for scientific or recreational purposes, acts affecting all the natural resources of the nation were passed. In May, 1908, Roosevelt convened a conference of governors at Washington, to consider problems of conservation. This was the birth of the conservation movement, which today is among the most important, fruitful, and forward-looking aspects of field biology. The forces of exploitation still constantly threaten, but they are now opposed by a large body of trained and educated conservationists, backed by a public which every year becomes more aware of the urgency of conservation needs.

The Nature-education Movement

Concurrent with the development of conservation, which was given impetus largely by governmental efforts, another movement was taking form with little or no governmental assistance. It was clear to many biologists that advances in the appreciation and understanding of nature would only be made by educating the citizens who hitherto had had no contact with biology. In the early 1900s, popular field guides began to appear, to aid in the identification of birds, butterflies, trees, ferns, and other flora and fauna. The Audubon Society, under Frank Chapman's able leadership, began to reach out into the public schools, where children in Junior Audubon Clubs learned about birds and eventually about other aspects of nature study. The Boy Scouts and similar groups, encouraged and guided by such able field biologists as Ernest Thompson Seton and Dan Beard, were exploiting the ingrained love of the out-of-doors, which is a part of American boyhood. At Cornell University, Liberty Hyde Bailey began the extension of nature study into the rural schools of New York State, and Anna Botsford Comstock embarked on a career of nature writing and illustration which brought this hobby to the attention of thousands of individuals.

These were only a few of the writers, speakers, and scientists who had a part in the development of the great nature-study movement. The varied approaches, the inclusion of both children and adults in these programs, resulted in a tremendous increase in appreciation of nature and in the number of amateurs engaged in bird study, botany, and similar pursuits. This in turn brought about an increase in the popular literature of biology (see Chap. 12). The crest of this wave of interest has perhaps not yet been reached, but nature study is certainly one of the major cultural trends of the twentieth century in America.

The Ecology Movement

With the rise of experimental biology, the naturalists of the early pioneer days began to fade from the scene. Most of the more obvious organisms had been described, and biologists were turning from the descriptive areas of biology to the laboratory disciplines. Advances in chemistry, medicine, and related fields paved the way for advances in physiology. The discovery of the basic facts of genetics near the end of the nineteenth century opened up a new experimental field, and observational natural history lost its appeal to these newer and more glamorous aspects of science. Theodore Roosevelt, enrolling in Harvard as a freshman biology major in 1876, was horrified to find that that great university offered essentially no training in field biology. "The tendency was," he later wrote, "to treat as not serious, as unscientific, any kind of work that was not carried on with laborious minuteness in the laboratory." Probably the same could have been said of most of the better-known American colleges.

But as the old natural history died, the seeds of a new natural history were being planted. About 1870 Ernst Haeckel, the great German biologist, defined a new branch of biology which he called ecology. This science, he said, would concern the total relations between organisms and their organic (biological) and inorganic (physical) environments. The challenge of this new field was quickly taken up by his colleagues, many of whom were already at work in studies embraced by his term, ecology. Forel in Switzerland was studying the ecology of lakes. Mobius, another German, established the community concept, which has played so important a part in the development of ecology.

In America, the new discipline found ready adherents. Interestingly enough, the early proponents of ecology were almost entirely Midwesterners. Stephen A. Forbes at the University of Illinois and the Illinois Natural History Survey made studies which are still classics in the field. Chauncey Juday and Edward Birge at the University of Wisconsin laid the groundwork for the study of limnology in America. H. C. Cowles at the University of Chicago, Frederic Clements and J. E. Weaver at the University of Nebraska, Charles C. Adams and Victor Shelford at the University of Illinois (the former moving to the New York State College of Forestry at Syracuse about 1914), led students into the study of this new branch of biology. They succeeded so well that in 1915 the Ecological Society of America was established, with Shelford its first president. The old naturalists had laid the foundation, and on it these and more recent ecologists have erected an imposing structure of knowledge.

Today, field biology is once again intellectually respectable. Field biologists are more numerous than ever before. Our knowledge of the lives and habits of animals, of the interrelationships of plants, animals, the soil, the climate, and other factors of the environment has increased manyfold. We cannot say now what important advances will emerge during the next half century, or what new trends in biology may open up new vistas to the field biologist. We may be sure, however, that so long as men feel a kinship with nature and a desire to know more of her secrets, field biology will flourish both as a profession and as a hobby.

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chapter 3

Taxonomic principles

To the layman, the word "taxonomy" is probably unfamiliar. To many biologists, taxonomy calls up visions of row on row of bottled specimens, shelf on shelf of herbarium sheets, tray after tray of stuffed specimens. The student wonders why he must learn those long and difficult Latin names and thinks of taxonomy as an exercise in memory.

These things are part of taxonomy, but if they were the whole picture, there would be no need for a chapter on taxonomy in a book concerned with field biology. The modern taxonomist may or may not be a field biologist himself. The modern field biologist may or may not be skilled in some aspect of taxonomy. But the study of taxonomy is basic to field biology, as it is to all biology, and field-gathered information is necessary to modern taxonomy, as it is to so many other disciplines.

In the early development of any region, taxonomy is the first and most important branch of biology. We can learn little of consequence about plants and animals until we at

Without system, the field of nature would be a pathless wilderness.

Gilbert White, "The Natural History of Selborne"

least have names for them. Oftentimes students think of taxonomy as a static or dead science, but there are still plenty of taxonomic problems in North America, even after some 350 years of effort.

First, we shall outline the principles on which our taxonomic system is based, then show how it relates to natural populations of plants and animals, and last, indicate how taxonomy is important to field biology and vice versa.

The broad field of study which embraces all aspects of organic diversity has been called *systematics* (Simpson, 1961). Within this broad field, the systematist has at least two distinct functions. One is the discovery, description, and placement into the classification system of unknown species and the refinement and clarification of relationships. This constitutes the field of *taxonomy*. Most taxonomists, however, serve another utilitarian function: the identification of known organisms for themselves or as a service to other biologists or to the public. The entomologists in museums, the botanists in state experiment stations, and other systematists as well may spend more of their professional lives in identifying known forms than in working with new ones.

The taxonomic function, however, is the basic one, so we may logically consider it first. Our present system of classification has been so firmly fixed for so many years that it seems very old. Actually, it has matured slowly over two hundred years but its details have become generally accepted the world over only in the present century.

It will be obvious to anyone who stops to think about it that the basic needs of a taxonomic system are disarmingly simple. Each species of organism must have a name, and the same name must not be used for more than one species. Each name must be universally understood, universally accepted, and universally used. Names must be as permanent as the nature of organisms will allow. And the classification system must be accepted throughout the world and used in a uniform manner everywhere. The present system of nomenclature at least attempts to meet these needs.

THE PRE-LINNAEAN PERIOD

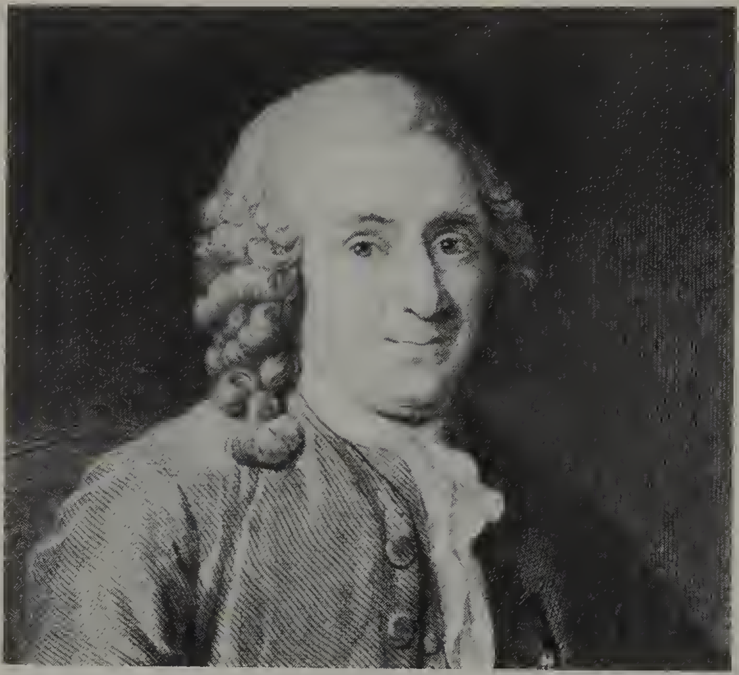
Before the middle of the eighteenth century, plants and animals were known by local (vernacular) names, which then, as now, varied from place to place. Scientists, of which there were few indeed, used Latin names, for Latin was the language of the learned. But there was no uniformity of usage. Communication was poor, scientists for the most part were retiring and untraveled, and it was therefore difficult for a scientist to keep up with the advances in other countries. At the time, there was an explosion of knowledge similar in kind if not in extent to that of our own day. The rapid expansion of the world's frontiers was bringing about the discovery of new species at a very rapid rate, and the Latin nomenclature was becoming unwieldy.

So long as only a few species were known, Latin names of two or three words had served to identify each one. Names used in authoritative and widely known monographs might even attain a fair degree of universality. But as explorations proceeded, more and more new forms were discovered in the far corners of the world. Botany and zoology were popular hobbies among the gentlefolk of those days, and many exploring expeditions took with them a collector or two to bring back the curiosities of nature for some sponsor at home. In order to describe those species and set them off in an adequate manner from similar species which were already known, new names had to be invented. The only solution that the scholars could devise was to add Latin words which were descriptive of the new species to the existing name of a similar organism. Names were no longer names but descriptions.

Suppose, for example, that a wild yellow rose existed in Europe which had been known for many years as *Rosa flava* (*Rosa*—rose, *flava*—yellow). Since this was the only yellow rose known to science, it would need no additional words to describe it to the satisfaction of any scientist. Let us suppose, however, that when exploring expeditions began to bring back organisms from unknown parts of the world, they brought back from the Far East two different kinds of yellow roses. The one with hairy leaves might be called *Rosa flava, foliis hirsutis,* while the other, which had smooth leaves, could be named *Rosa flava, foliis glabris.* Meanwhile, the original flower, no longer the only yellow rose known to science, would have to be renamed—perhaps *Rosa flava, europea.* If, then, an expedition to Australia brought back three more yellow roses, all with hairy leaves but varying in size and shape of leaves, another modifying name would have to be added. In precisely this manner the names of organisms could, and did, proliferate, until many organisms had names like the one accorded to the common honeybee: *Apis pubescens, thorace subgriseo, abdomine fusco, pedibus posticis glabris utrinque margine ciliatis* (the downy bee with the thorax gray below, the abdomen fuscous, the hind legs hairless but with the margins ciliated). A fine mouthful indeed for the practicing taxonomist to commit to memory!

LINNAEUS AND BINOMINAL NOMENCLATURE

Obviously a system of this kind must eventually break down of its own weight. Workers in various countries were working toward the idea of a genus with several similar species grouped together. Bauhin in Switzerland and John Ray in England were groping toward a system which would permit a short simple name to be applied to each species. But the Gordian knot was finally cut by a young Swedish botanist, Carl von Linné, later known by the name Carolus Linnaeus (Fig. 3-1). As an eager young student of natural history and medicine at



Charles Knight and Company, Ltd., London

Fig. 3-1 Carolus Linnaeus, 1707–1778.

the University of Upsala, he decided to devise a classification system for all organisms. Enlarging and improving upon the ideas of his predecessors, he finally formulated the system which still bears his name. In brief, his idea was to give to each species of plant and animal a name consisting of two Latin words—the name of the genus (generic name) and a trivial or species name. The first biologist to discover a previously undescribed species was to choose a name in accordance with the Linnaean system. This name, with a description of the organism, was to be published in a scientific journal or other publication where other workers might read it. The name thus selected, along with the name of the describer, would thenceforth be the only acceptable name for that species. Any worker who wished to know to what organism the name referred could, theoretically at least, find out by reading the description. In early days descriptions were written in Latin, but descriptions in other languages are today widely used and quite acceptable in zoology. Botanists still cling to Latin descriptions.

This system of *binominal nomenclature* * was first used uniformly by Linnaeus in his "Species Plantarum" (1753). For animals, the first consistent usage was in his "Systema Naturae," 10th edition (1758). These two dates mark the birth of modern botanical and zoological nomenclature respectively. Names used before then have no standing in nomenclature unless Linnaeus retained them in these two works.

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* Many authors use the word "binomial," but as Mayr et al. (1953) have pointed out, correct etymology demands the use of *bi* (two) + *nomen* (name), hence *binominal.*

The advantages of this system can readily be appreciated. The name of the honeybee was reduced from the 12 words given above to *Apis mellifica* Linnaeus, and other names benefited in the same manner. The system met with general, though not immediate, acceptance among biologists, who could scarcely fail to appreciate the advantages of its simplicity. During his long lifetime (1707–1778) Linnaeus named and described thousands of species of plants and animals which still bear his name.

Hierarchical Classification

The various forms of life known to Linnaeus not only were described and named, but also were arranged by him in hierarchical succession of groups. Indeed, Linnaeus's contributions to a natural arrangement of plant groups were nearly as important as his development of the binominal system. Species which seemed similar were placed in the same genus. Similar genera were placed together to make up a family. Families were grouped into orders, orders into classes, classes into phyla (singular, phylum). Modern usage is somewhat different from that of Linnaeus in the number and scope of these terms, but the principles of the system remain essentially as he designed them. The phyla were grouped into two kingdoms, plant and animal. Taking, for example, the widespread and well-known American robin, the entire classification would be:

- Kingdom: Animal
  - Phylum: Chordata
    - Class: Aves
      - Order: Passeriformes
        - Family: Turdidae
          - Genus: *Turdus*
            - Species: *migratorius*

Scientific name: *Turdus migratorius* L.

The Species Concept

In general, taxonomic groupings are admittedly artificial, set up for the convenience of biologists. The species, however, represents a natural unit: a population of organisms, freely interbreeding, but not freely interbreeding with other similar groups, and resembling each other more closely than they resemble members of other populations.

This definition of a species will not satisfy everyone; indeed, Simpson (1961) argues cogently that no one definition can be universally accepted. Nevertheless, it will serve as a point of departure for a discussion of the criteria on which species are based. The most common criterion is reproductive isolation. Mayr et al. (1953) defined species as groups of organisms reproductively isolated from other such groups. This criterion is generally useful if we recognize that isolation may break down and that hybridization occurs quite commonly (Fig. 3-2).

Simpson (1945) pointed out that our concept of a species is actually based on inferences drawn from a small sample of the population and is, to that extent, a subjective concept based on a real morphological and genetic entity which is not generally observable as a whole. In a few unusual cases, we may be able to observe the entire existing population of a particular species. For example, all of the whooping cranes in existence, except for a few in zoological gardens which are easily seen (Fig. 3-3), gather in winter at the Aransas Wildlife Refuge in Texas. Therefore, in theory at least, any biologist might study the species *Grus americana* in its entirety. Obviously, this is a very special case, and we must ordinarily be satisfied with examination of a small proportion of the totality of any given species.

Perhaps it is less important to be able to state clearly just what a species is than to know how taxonomists arrive at their conclusions as to whether a given population represents a distinct species. In making such decisions, taxonomists generally use at least three kinds of information which we have already hinted at, but which we now present in some detail.

First, a species must be *morphologically distinct* from other similar forms. There are in certain groups of organisms physiological species without noticeable morphological variation. Taxonomists call them sibling species. In microbiology, morphologically indistinguishable organisms may show

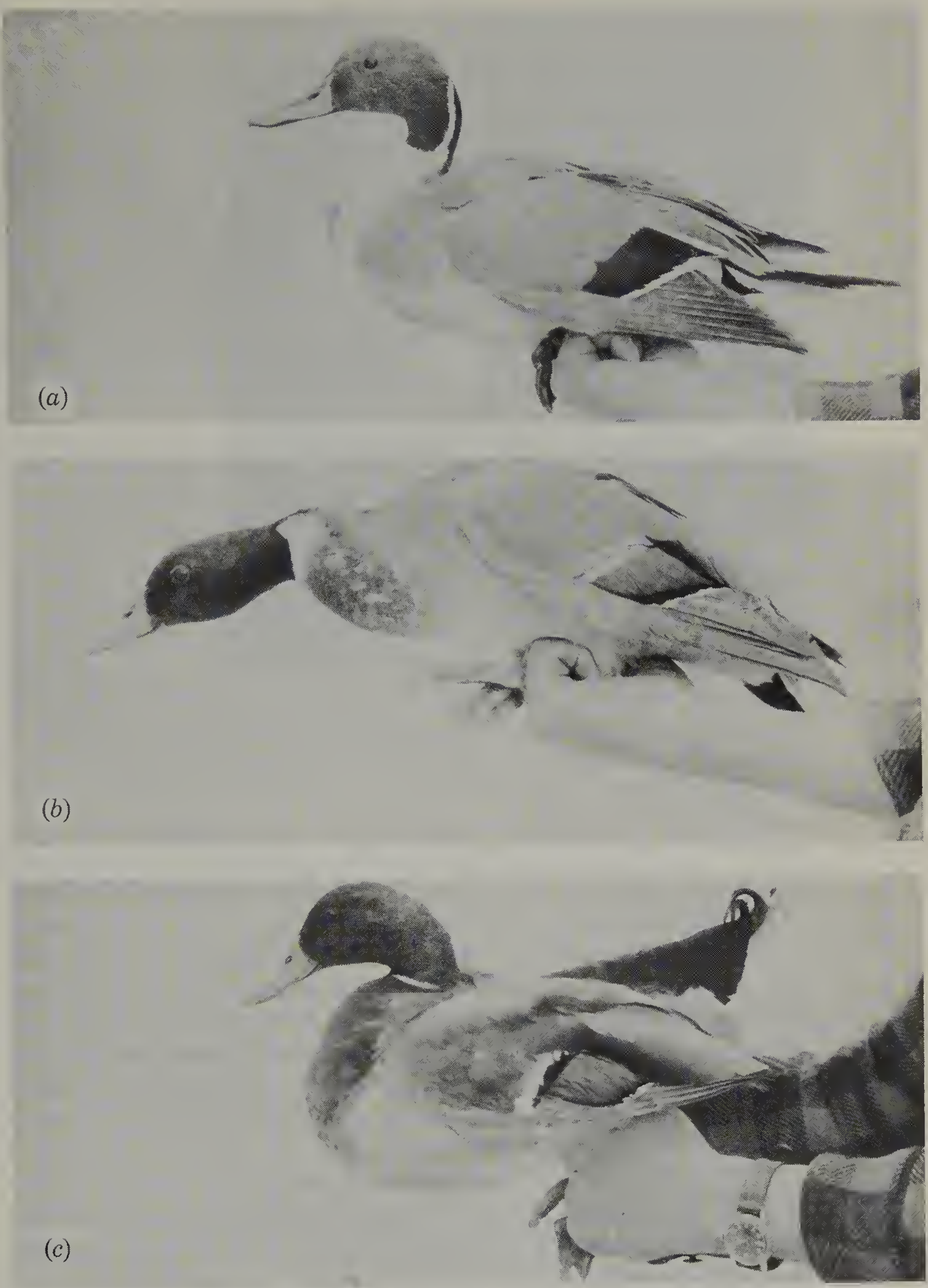

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Fig. 3-2 Hybridism in the duck family. (*a*) Male pintail. (*b*) Male hybrid between mallard and pintail. (*c*) Male mallard.

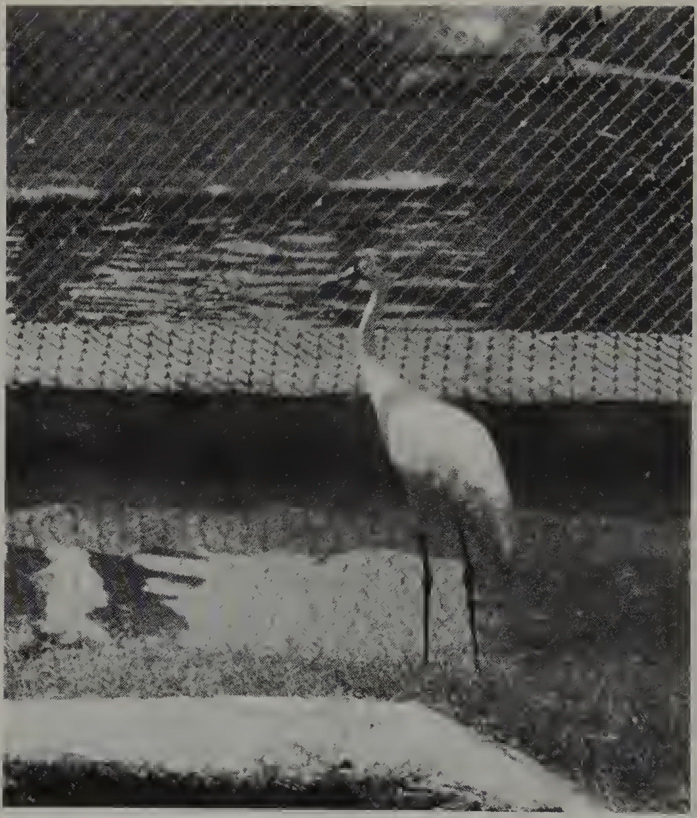

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Fig. 3-3 One of the few remaining whooping cranes, *Grus americana,* in the San Antonio Zoo.

quite different characteristics and be good species. In general, however, we must be able to see some differences between organisms of different species. It would be quite impossible to use preserved specimens on any other basis.

Second, as we have noted, different species do not interbreed freely. We may think of this as *genetic distinctness.* We have already indicated there are exceptions to this genetic isolation, but when they occur they cause taxonomists to take a long hard look at the two interbreeding forms and to consider the possibility that they ought not to be considered as separate species.

A number of well-documented cases may be cited. Mallard ducks and black ducks will, in captive flocks, interbreed freely. Unlike many hybrids, they are quite fertile, and the resulting population is a peculiar assemblage of intergrading characteristics. Blue-winged warblers and golden-winged warblers frequently interbreed in nature, and probably a large percentage of the recognizable members of each species have some family history of hybridism. Some ornithologists have therefore suggested that the two ought not to be considered distinct species because of this interbreeding.

The reason for this inconsistency in nature (from our human point of view) is the fact that the process of speciation is a slow one. If two populations have been separated long enough to develop some differences but not long enough to have developed effective isolating mechanisms, either behavioral or genetic, it is likely that they will interbreed when they come together. Quite possibly the cases above are examples of forms which were once geographically isolated but have not developed enough genetic differences to prevent successful hybridization. In the case of the ducks, isolating mechanisms must exist which usually work in nature, since natural hybrids are rare. In the case of the warblers, neither genetic nor behavioral isolating mechanisms are effective, and it is quite possible that the two populations are remerging into a single species.

Third, a species does not occupy the same geographical and ecological range as its closest relatives. At places, the ranges may overlap, and ecological preferences may be similar, but differences can usually be found. Biologists have for many years accepted the competitive exclusion principle that no two species which are identical in their demands upon the environment can exist in the same range. In theory, one species would be more efficient and in time would eliminate the other. Actually, this has developed into a kind of exercise in circular logic. If two similar species are found together, a biologist is tempted to conclude that they must have different ecological demands or they could not occur together. However, it is well known that two parasites, whose demands are certainly identical, can occur on or in the same host, and arguing about whether a difference of a few millimeters in location constitutes a difference in ecological range would seem to be quibbling. In short, this biological truism needs some qualification (see, for example, Klopfer, 1962, p. 37).

Although all three of these factors, morphological, genetic, and spatial, have a part in our determination of species, it is evident that morphological differences, which are readily observed, are the more useful criteria in actual practice. Most species show morphological distinctions of sufficient magnitude that they are easy to recognize. A few species in any group will give us trouble because morphological characteristics are similar in closely related species. Some examples are the Chrysomelid beetles, or the flycatchers of the genus *Empidonax.* Still, when we start to learn about species, we lean almost entirely on morphological differences.

The taxonomist, too, must lean heavily on morphological characteristics in distinguishing unknown species, although he may use other factors, including behavioral characteristics, to support his conclusions. His description, on which the recognition of the species is based, is typically entirely morphological. Modern descriptions may include some information about behavior, about songs or other vocalizations, food habits, host preference of parasites, and other items which might be of value in evaluating the correctness of his conclusions. But the major weight of evidence continues to be on differences which can be seen or measured, and it is difficult to see how this situation can be markedly changed in the foreseeable future.

The Subspecies Concept

As our knowledge of organisms has increased, it has been necessary to modify the hierarchical arrangement shown above by the addition of other groupings. Subphyla, superfamilies, subfamilies, and other groups have been added for the convenience of the taxonomist. These are of little importance to the non-taxonomist, except for the subspecies. The addition of this category has converted the binominal system of Linnaeus into an essentially trinominal system, although it may be said that some taxonomists do not approve of this trend. The subspecies was added because widespread species often show consistent regional variation in minor characteristics such as size, coloration, or habits, and such forms may be given a third, or subspecific, name. This recent trend in taxonomy is of importance to the field biologist, who may be called upon to evaluate the probable validity of subspecies on the basis of his knowledge of their natural history. It will be necessary, therefore, to give some further consideration to this concept.

Mayr et al. (1953) define subspecies as "geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of a species." It will be noted that this definition has two requirements: geographical distinctness and taxonomic (morphological) distinctness. Genetical distinctness is not expected, since members of different subspecies which belong to the same species can interbreed freely if placed together. If there is no evidence of interbreeding, forms which are morphologically similar are at once suspected of representing distinct species. It is often impossible to prove that interbreeding will occur by placing the animals together in captivity, for they may not breed under artificial conditions. In nature, however, it is possible to deduce interbreeding by the discovery of *intergrades*—individuals which have either morphological characteristics midway between those of two subspecies, or some of the characteristics

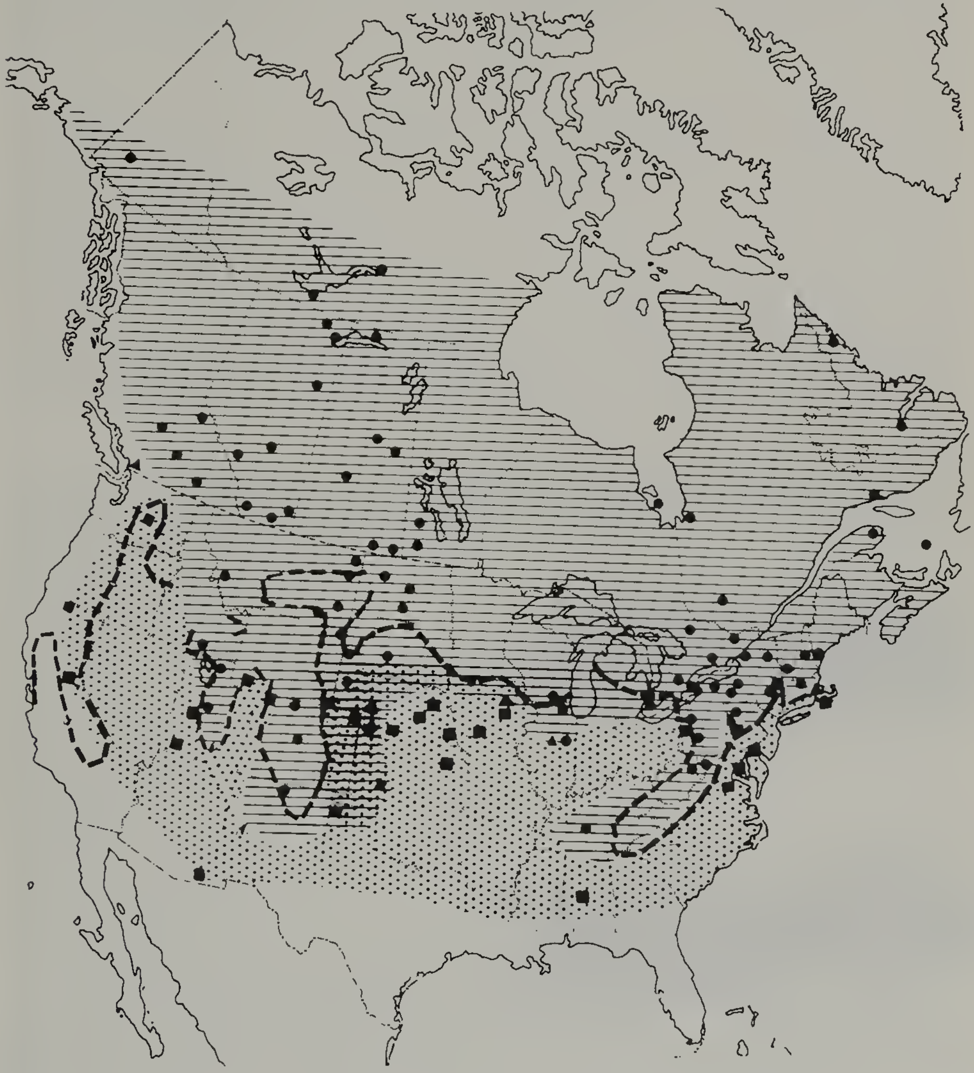

Fig. 3-4 Subspeciation in a species of flea, *Epitedia wenmanni.* Large dots represent specimens of the northern subspecies, *Epitedia wenmanni wenmanni;* squares—specimens of the southern subspecies, *Epitedia wenmanni testor;* triangles—specimens intermediate between the two subspecies, known as intergrades. Note that such intergrades occur at various places along the line where the ranges of the two meet. Map from Benton, *J. Parasit.,* 41(5):493.

of both. When two subspecies meet over a large area, intergrades may be expected to occur throughout that area (Fig. 3-4). In the case illustrated by this figure, the two populations had originally been described as two species, but the presence of large numbers of intergrades where the two ranges come together indicates their subspecific status.

The subspecies concept, incidentally, has been most fully developed among zoologists but has met with some resistance among botanists. For this reason, the illustrations used to demonstrate the concept are all taken from the animal kingdom.

It has been pointed out that geographical separation is one of the characteristics of subspecies. This separation, however, may occur only in the most general terms. In parts of the Northeast, two subspecies of the deer mouse, *Peromyscus maniculatus* (Fig. 3-5), are separated only by virtue of the fact that one prefers grasslands and open fields while the other prefers forests. This has occurred, apparently, because a prairie population has worked its way eastward in cleared areas until it has invaded the territory of the other subspecies. The

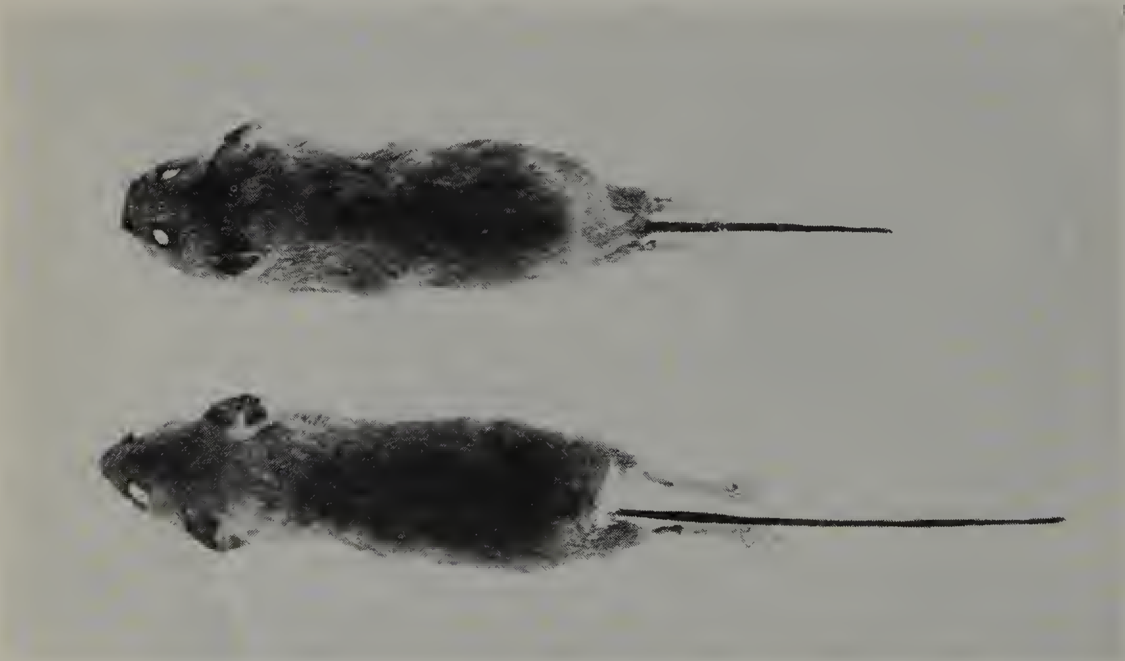

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Fig. 3-5 *Peromyscus maniculatus gracilis* (bottom) and *Peromyscus maniculatus bairdii* occur over many hundreds of square miles of the same geographic range but are usually well separated ecologically; *gracilis* is a woodland form, *bairdii* prefers open land.

same phenomenon has occurred in the case of the Traill's flycatcher (Parkes, 1954). This latter case is further complicated by the fact that morphological differences between the two forms concerned are very small indeed. In life they can be readily distinguished by voice and habits, but study skins can be differentiated only with great difficulty.

Thus a subspecies may not be geographically isolated in the usual sense of the term. Mayr et al. (1953) elude this difficulty by the use of the term *microgeographical* to indicate that the two forms occur in different ecological areas. For practical purposes, however, two subspecies which occur over several hundred square miles of the same territory can hardly be said to show geographical isolation. It would be impossible to plot on a map of ordinary size the ranges of the two subspecies of deer mice or of Traill's flycatcher mentioned above. It seems simpler to say that these subspecies are ecologically separated rather than geographically separated. Another difficulty with the subspecies question is the effect of environment on color, size, and similar characteristics. If variations are not genetically fixed, the organism possessing them would not be considered taxonomically distinct, but this is not always easy to find out. No doubt there are many "subspecies" which have been described on the basis of variation due to environmental rather than genetical differences. There are, for example, more than two hundred described subspecies of the pocket gopher, *Thomomys umbrinus,* and similar numbers for many other species.

Ever since its inception there have been objections to the subspecies concept. Although it had been generally used for more than half a century, it again became the center of controversy during the last decade. Wilson and Brown (1953) criticized the concept as "the most critical and disorderly area of modern systematic theory." They and other critics have called the use of subspecies inefficient, superfluous, arbitrary, and capricious.

Objections to the use of trinominals generally fall into a few standard categories. First, there are no generally acceptable criteria for recognizing subspecies. The same complaint might be made, of course, about any taxon, but it is most often used in regard to subspecies. Second, critics feel that describers of subspecies emphasize minor differences and ignore major similarities, thus obscuring rather than illuminating relationships. Third, three names are obviously harder to remember and take up more space than two, hence are a burden to the taxonomist.

At least one taxonomist (Michener, 1963) has gone still further and suggested that the ultimate in simplicity is a uninominal nomenclature. If a name is only a name and not in any sense a description, only one name is needed. The difficulty of finding suitable names for the more than one million known species of organisms, however, might be a limiting factor in any such scheme.

Despite persistent objections, the subspecies concept appears to be firmly embedded in modern nomenclature. The numerous arguments against it certainly have weight, but to most taxonomists its advantages outweigh its disadvantages.

The Development of Nomenclatural Codes

The work of the post-Linnaean taxonomists using the Linnaean system brought rapid progress in classifying the vast numbers of plants and animals. Complications soon arose, however, because of the lack of uniformity of usage and the absence of generally accepted rules. Some workers changed names which had been proposed by earlier taxonomists because of apparent unsuitability. For example, if our rose, *Rosa flava,* named after its yellow flowers, was found by a later worker to be based on an abnormal individual, the flowers of normal plants being red, he could rename it *Rosa rubra.* If such changes were allowed, it was a short step to changes of names because of national prejudices or personal dislikes, without regard to the suitability of the name. Furthermore, not all workers accepted the Linnaean system readily or consistently, and among those who did there was no uniformity of method in adapting it to their own peculiar problems. Some workers developed personal rules of usage, but these differed in different countries and even within the same country. It began to appear that the ascent from chaos was only a temporary one.

By 1840, the need for a uniform code of usage was recognized to the extent that a committee was formed in England to draw up a suitable set of rules. The Stricklandian Code, so named after the chairman of the committee, Hugh Strickland, was an outstanding accomplishment. The committee comprised representatives from many fields, including most of Britain's foremost biologists. The code which they produced was not universally accepted, but it succeeded in stimulating biologists in other countries to draw up different and better codes. By 1895 there were perhaps a half-dozen major codes in use, including the American Ornithologists' Union Code, the so-called International Code, the Dall Code, and the Stricklandian Code. The need of a genuine international code was obvious, and zoologists accepted one, written by an international committee, in 1901.

Botanists, meanwhile, were proceeding separately to establish a standard world nomenclature. The first International Botanical Congress met in Paris in 1867 and adopted a set of rules, mostly suggested by the Swiss botanist Alphonse de Candolle. This set of rules, usually known as the Paris Code, was generally accepted, but a group of American botanists did not find it to their liking and formulated a code of their own. The Vienna Congress of 1905 was expected to solve the difficulties between these opposing forces, but no satisfactory results were achieved. The stalemate continued until 1930, with American botanists more or less evenly divided between supporters of the International Code and users of the American Code. At last, in 1930, the Fifth International Botanical Congress at Cambridge, England, succeeded in bringing the major disagreements to a discussion and vote, and the American Code was abandoned.

The next logical step might seem to be a uniform code for both botanists and zoologists, but this may be long in coming. Because of the many differences between botanists and zoologists in nomenclatural usage, and because of the inevitable confusion which would result if either group accepted the usage of the other, most taxonomists are not anxious to make the change. As mentioned above, descriptions of plants are made in Latin, while any language may be used in describing new species of animals. In botany, tautonymy (the use of the same word for the genus and the species) is forbidden. Acceptance of this rule by zoologists would require the change of many familiar names, such as *Bison bison, Gallus gallus,* and *Turdus turdus.* Furthermore, many plant genera have the same names as animal genera. If a uniform nomenclature were adopted, either the plant or the animal would have to be renamed. Possibly it may be less trouble to maintain two systems.

The international rules of nomenclature, if we were to include both plant and animal, would nearly fill a book this size. Some basic provisions, however, are identical or similar in both groups, and a few of the more important ones are worthy of note.

One of the basic principles of nomenclature has always been *priority;* that is, the name first applied to a species is the valid name. (Of course, names may be changed for various reasons, especially generic names, but in theory at least the trivial or species name should be stable.) This system began with the names used by Linnaeus in 1753 and 1758 respectively and applies to other names of new species described since that time. In general, this rule has the effect of stabilizing the nomenclature and placing credit where credit is due. There have been numerous objections, because it has happened not infrequently that old names, long buried, have been resurrected and have replaced well-known and long-used names. To avoid this, it has been customary for the International Committee on Nomenclature, either botanical or zoological, to settle arguments over long-unused names. If it seemed to this committee that strict use of priority would be more confusing than helpful, they could declare the familiar name a *nomen conservandum*—a conserved name—one which is not to be replaced on the basis of priority. Dozens of scientific names which otherwise would have been replaced on the basis of strict priority have been retained as *nomina conservanda.*

The priority system was further limited at the International Zoological Congress of 1958. The revised code adopted at this meeting provided for a 50-year limit on priority. Any name which lies unused for 50 years and is then rediscovered is considered to be a *nomen oblitum*—a forgotten name—and is not to be used. Other important provisions of this code are discussed by Follett (1963).

Despite the best efforts of taxonomists, names of organisms can never be completely stable. Revision of a group in the light of new knowledge may cause the transfer of a species from one genus to another, the erection of new genera, or the reduction of genera which had been erected previously. Trivial names, of course, except for minor emendations of endings to match changes in gender of the genus, remain constant unless there is a change because of priority. Thus the American robin was described by Linnaeus as *Turdus migratorius.* Later it was known as *Merula migratoria,* then as *Planesticus migratorius.* Most recently it has been restored to the genus *Turdus.* It is this juggling about from genus to genus which makes taxonomic work confusing to the layman, but the aim is a stable nomenclature.

In order to have nomenclatural standing, a name must be more than just a name. First, it must be printed in a publication which is placed on sale or is otherwise made available to any interested person. Furthermore, it must be accompanied by an adequate description, so that future workers can determine from the description what species was involved. A name without an accompanying description or with one so inadequate that it is not evident as to what organism is being described is a *nomen nudum* and has no standing in nomenclature. For example, the long-tailed weasel of the eastern United States was named *Putorius noveboracensis* by James DeKay in his volume on the mammals of New York. DeKay did not include any description; the name is therefore a *nomen nudum*. It was rescued from oblivion, however, by Emmons, who in a similar work on the quadrupeds of Massachusetts used the name and gave an adequate description. This form has since been reduced to subspecific status, so that its present scientific name is *Mustela frenata noveboracensis* (Emmons). The parentheses around the name of the describer indicate that the species has been transferred to a different genus or that the name has been changed in some way since it was first applied.

NEW APPROACHES TO TAXONOMY

There is, of course, no way to make names completely stable. Taxonomy is by no means a stagnant branch of science, and new approaches are bringing fresh insight into difficult areas of taxonomy. Chemotaxonomy, the study of relationships by chemical analysis of plant and animal parts, has shown great promise. Analysis of blood serum has demonstrated that taxonomic relationships are accompanied by similarities in blood constituents. Chromatography permits recognition of minute quantities of chemicals and also permits ready comparison of different materials. Thus one can run chromatograms of different plant or animal parts (seeds, muscle tissue, and so forth) and easily see both similarities and differences. Microanalytical techniques are increasingly important in chemistry, and the results have proved of interest in many fields, including taxonomy (Alston et al., 1963).

For the most part, these techniques have provided relatively few surprises. In some cases, they have solved problems in which taxonomists had held divergent views. In other cases, they have supported the weight of evidence gained from morphological studies. There is no doubt that such techniques will continue to be brought to bear on the more difficult problems of taxonomy and will aid in their eventual solution. Contrary to some rumors, taxonomy is not dead. Many hundreds of species await discovery, and many little-known species need further study. The modern taxonomist can make use of those techniques which his predecessors lacked and can thus expect to reach a more sound position in taxonomic work.

For many years, mathematically minded biologists have felt that there should be some way to determine taxonomic levels mathematically and to develop a taxonomic system which might result in giving species numbers rather than names. For example, some workers have used the 75 per cent rule in recognizing subspecies. In other words 75 per cent of the members of the two populations must be recognizably different in order to have subspecific status. Of course relationships are directly correlated with the number of similar genes, so that such an approach has a theoretical basis, but it is hardly practical at the present time. Nonetheless, a considerable number of taxonomists are currently interested in utilizing the new methods of data processing and statistical analysis, and the field has undergone considerable recent development. A detailed discussion of the accomplishments and methods of this numerical aspect of taxonomy is given by Sokal and Sneath (1963).

The Type Concept

In the days of Linnaeus, the idea that any one organism was a type of a specially created species was generally accepted. While this philosophical idea is no longer prevalent, the use of a specimen as typical of a species is universally acknowledged. It might be more accurate to say that one specimen is selected as the type of a particular name, which in turn represents a species. In practice, the describer of a new species chooses one specimen as the *type specimen*, or *holotype*. This is a specimen which the describer considers typical. It is usually a male in the case of bisexual animals; a specimen of the opposite sex is designated the *allotype*.

The function of the type specimen is an important one, and though the system never functions perfectly, almost all taxonomists agree that it would be less perfect without types. The type specimen provides a permanent reference point for future taxonomists. If any future worker wants to be absolutely certain what organism the describer of a species referred to, examination of the type will answer his question. If later information shows that several species were included in the specimens on which a description was based, a study of the type will show to which species the name must be applied. The other species can then be assigned other names. Indeed, the type is so important that the code adopted in 1958 authorized the designation of a neotype (new type) in cases where the original type specimen has been lost or destroyed and a taxonomic problem has arisen which would be made easier by a study of the type.

The systematic function of the taxonomist (or the taxonomic function of the systematist) is, then, a matter of considerable complexity. The identifying function is usually somewhat more straightforward, though it is not without its complexities. It depends upon an intimate knowledge of the group of organisms concerned and in most cases the use of a taxonomic key, a tool to which we must now give some attention.

The Taxonomic Key

Once the classification system became relatively stabilized, the knowledge of plants and animals increased rapidly. Thousands of new forms were described, monographs of groups were written, hundreds of workers in all parts of the scientific world needed means to identify the organisms in the groups of their interest. No one could remember them all unless he was dealing with a very small group. To read thousands of descriptions until one was found which matched the organism one was studying was not practical. The solution was development of the taxonomic key, one of the most useful and essential tools which the biologist must learn to use. The taxonomic key is not an object used to open doors, although figuratively speaking it opens doors which might otherwise remain locked. In its simplest form, the key consists of a series of numbered couplets, each listing characteristics that the organism may possess. The two parts of the couplet are mutually exclusive; the organism to be keyed cannot fit both parts. By successively choosing the correct part of the couplet and moving on to the couplet that the correct choice indicates numerically, one can trace an organism to its correct identification. The user will find that his facility with any key will gradually increase, and that there is much variation in keys; the principles of use, however, remain the same. A key to the members of the squirrel family in the northeastern part of the United States (Fig. 3-6) might run like this:

1. Length 18 inches or more. (2)
1. Length under 15 inches. (4)

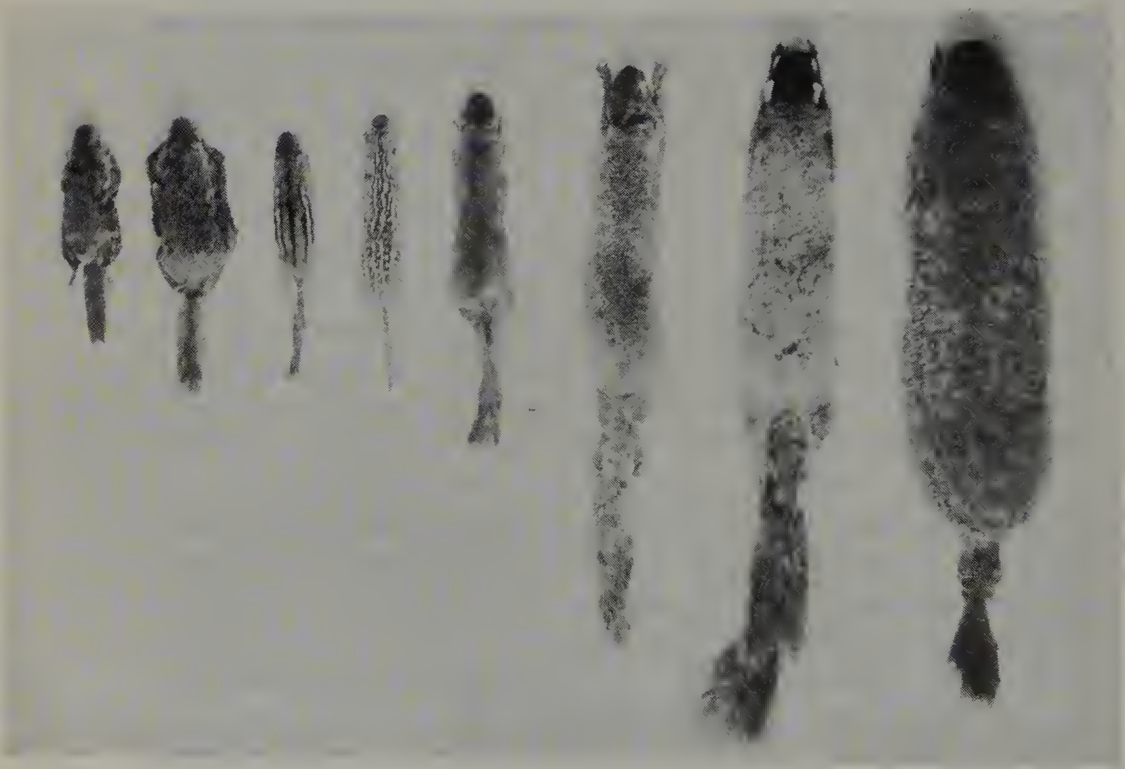
2. Body stout, tail much shorter than body. (*Marmota monax*, woodchuck)

2. Body relatively slender, tail about as long as body. (3)

3. Gray above, white below, rusty on sides and head. (*Sciurus carolinensis*, gray squirrel)

3. Gray to black, tail rusty beneath. (*Sciurus niger*, fox squirrel)

4. Lateral membrane between front and hind limbs. (5)



Allen H. Benton

Fig. 3-6 Squirrels (family Sciuridae) of the eastern United States. Left to right, southern flying squirrel, *Glaucomys volans;* northern flying squirrel, *Glaucomys sabrinus;* eastern chipmunk, *Tamias striatus;* thirteen-lined ground squirrel, *Citellus tridecimlineatus;* red squirrel, *Tamiasciurus hudsonicus;* gray squirrel, *Sciurus carolinensis;* fox squirrel, *Sciurus niger;* woodchuck, *Marmota monax.*

4. No lateral membrane present. (6)

5. Length 10 to 12 inches. (*Glaucomys sabrinus,* northern flying squirrel)

5. Length 8 to 9.5 inches. (*Glaucomys volans,* southern flying squirrel)

6. Back prominently striped. (7)

6. Back not prominently striped, red above, white below. (*Tamiascurus hudsonicus,* red squirrel)

7. Color olive green with many light stripes. (*Citellus tridecimlineatus,* thirteen-lined spermophile)

7. Color gray and reddish, with black and white stripes. (*Tamias striatus,* chipmunk)

Now let us suppose that you find a squirrel that you do not know. Using the key, you find that it is less than 15 inches long, so you go to the fourth couplet; it has no lateral membrane, so you go to the sixth couplet; its back is prominently striped, so you proceed to the seventh couplet; it is a gray and reddish animal with alternating black and white stripes. This brings you to the chipmunk, this is the name of your specimen.

To check the correctness of your keying, it is wise to compare the animal with more complete descriptions in some standard identification manual and with a photograph or drawing, if such can be obtained. Keys and identification manuals are available for almost any group of organisms (see Appendix). Some are highly technical and require advanced knowledge of biology. Others are mere picture books which in all too many cases are incomplete, inaccurate, and misleading. The field biologist will find it to his advantage to possess good manuals for the groups in which he is interested, and should familiarize himself thoroughly with the characteristics used in the keys, or in otherwise identifying the various species. Only in this manner can he become capable of intelligent field work.

Identification of organisms is a necessary means to an end, but it should not be considered an end in itself for the field biologist. Having achieved the ability to recognize the species with which he comes in contact, the average amateur, or occasional professional biologist, comes to a standstill. In so doing he sacrifices both enjoyment and usefulness, for much can be accomplished beyond this point if a few techniques are learned and a few principles understood. It will be our aim in the next few chapters to explore some of these principles and to review some of the important techniques.

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chapter 4

Energy transfer in natural communities

In a sense, this chapter is the story of sunshine; more precisely, of the things that happen to the energy of sunshine after it reaches the biosphere. Without this energy, life on earth would be impossible. Life, all life, is an expression of energy, and our only source for that energy is the sun (Fig. 4-1). The manner in which energy enters, passes through, and leaves the natural community is one of the basic aspects of biology.

This is not a new field; even the ancients wondered and theorized about vital force, though perhaps they would not have thought of trying to measure it. The early ecologists who tried to bring some degree of precision to the study of energy flow were handicapped by lack of suitable instruments and techniques. Even modern instruments leave something to be desired, but we can do much more than was possible only a few years ago, and the problems now appear possible of solution, though laborious.

To some extent, the precise determination of energy flow

On a summer's day Wolstanbury Hill is an island in sunshine;
you may lie on the grassy rampart, high up in the most delicate air
. . . all warmly lit with sunshine, deep under liquid sunshine
like the sands under the liquid sea.

Richard Jeffries, "The Open Air"

is a laboratory discipline. The tools and techniques have not yet been developed to make field studies entirely satisfactory. The flow of energy is a natural phenomenon which cannot be understood without knowledge of the natural situation, and what we understand is of little use unless we can apply it to the natural situation. It is therefore a part of field biology, though here, as in many other cases, the field biologist must carry out part of his studies under the controlled conditions of the laboratory.

Some Basic Facts about Energy

Energy occurs in many forms: heat, light, matter, electricity, and so forth. That which we can use comes indirectly from the sun. Vast quantities of heat, light, and X-irradiation are given off by this giant luminary, and a small portion of this energy reaches the earth. Most of the heat and ultraviolet

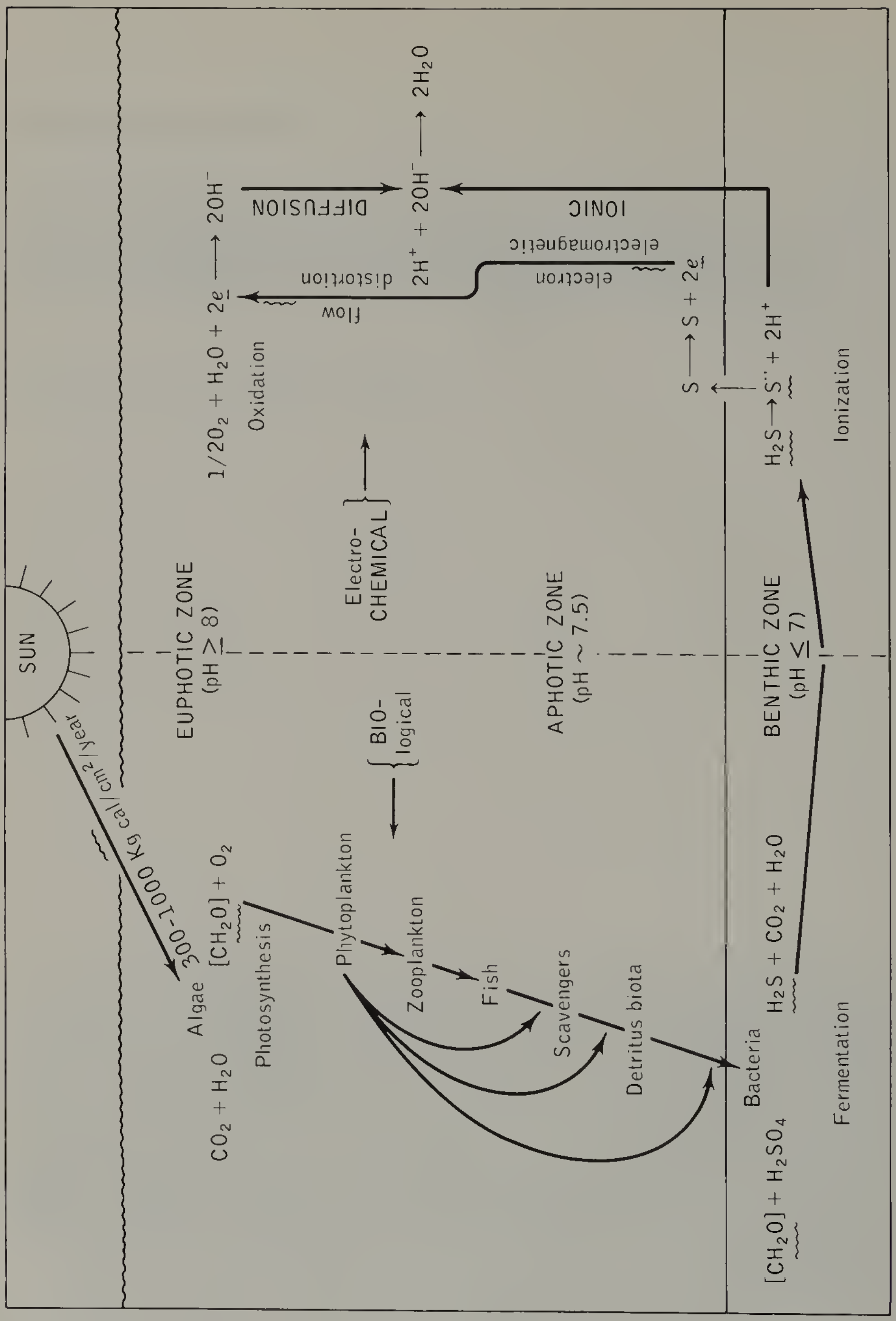


Fig. 4-1 A diagrammatic summary of energy exchanges in an aquatic community. Courtesy of Dr. Frederick Sisler.

light are absorbed by the atmosphere and never reach the earth's surface. The X-irradiation which reaches the surface is useless to us (and indeed, may even be harmful). From the remaining light comes all our useful energy. But only the green plants, among all earth's organisms, can transform this solar energy into stored energy in chemical form. The sunlight, striking bits of chlorophyll, causes electrons to become "excited" and to start a reaction which eventually changes carbon dioxide and water into sugar. Upon this remarkable process all life on earth depends.

The study of energy belongs perhaps in the field of physics rather than biology, so we must borrow some of the information, methods, and tools of physics in our explanation of energy flow. Two basic laws of physics must first be clearly understood: the first and second laws of thermodynamics. The first law is sometimes spoken of as the *law of conservation of energy.* It states that, in any isolated system, the amount of energy is constant. Energy cannot be destroyed, only changed from one form to another. Nor can it be created, only transferred from one part of the system to another.

A natural community, of course, is not an isolated system. It is constantly adding energy from the sun and losing energy through heat and organic processes. So long as the sun continues to provide energy, the system will continue to operate. Here, however, the second law of thermodynamics enters the picture. This law, known as the *law of entropy,* states that in an isolated system, there is always an increase in entropy, i.e., in the degree of disorder in the system. This tendency to disorder is reflected in the degradation of energy into successively less useful forms. A waggish scientist once said that according to the first law of thermodynamics you can't win, while the second law says that you can't even break even.

Within the natural community, then, there is a loss of useful energy every time a green plant converts solar energy into the potential energy of stored food. Every time a herbivore eats a blade of grass, a large part of its stored energy is lost as heat or waste materials. When a predator feasts on this same herbivore, much of the energy in the herbivore flesh is lost in the transformation into predator flesh.

For this reason, it takes a great deal of vegetation to support one large herbivore, and many herbivores to support one large carnivore. These facts are often expressed in the form of a *biotic pyramid* (Fig. 4-2), often referred to as the pyramid of numbers, or the Eltonian pyramid after the English ecologist, Charles Elton, who first proposed it.

This diagram shows, first, that green plants are the basic organisms; without them, there could be no addition of energy to the system, and it would soon fail to function. Green plants, therefore, are called *producers.* Of course, according to the first law of thermodynamics, they do not actually produce energy; they only transform into usable form the energy which comes to earth from the sun.

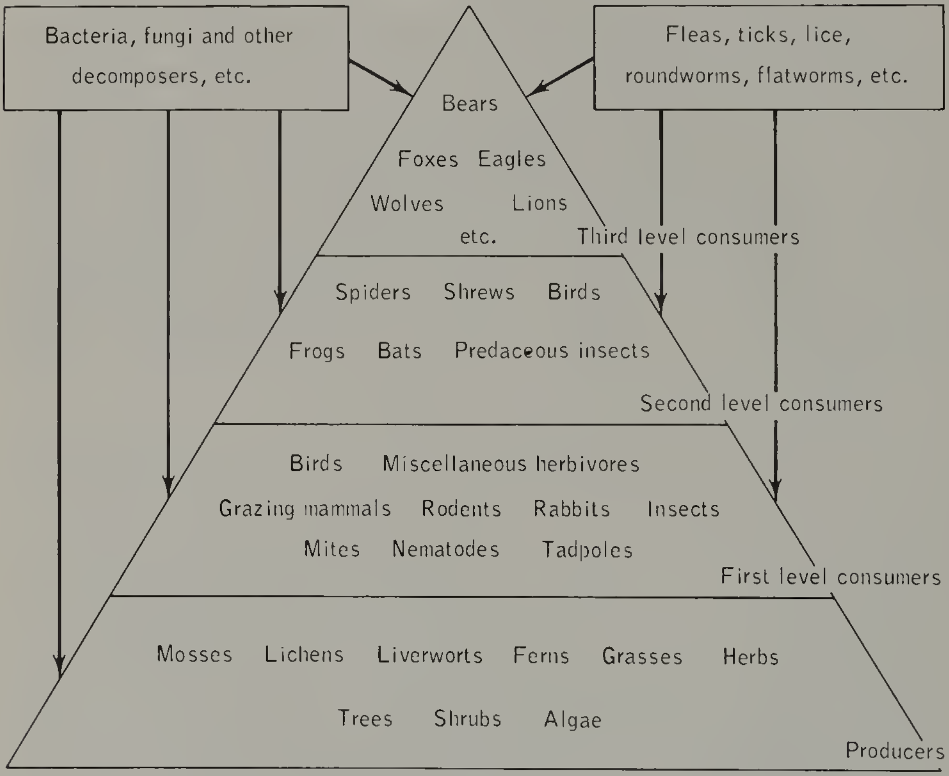
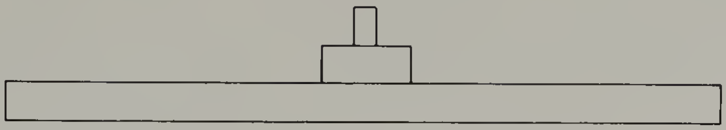

Bacteria, fungi and other decomposers, etc.
Fleas, ticks, lice, roundworms, flatworms, etc.
Bears
Foxes Eagles
Wolves Lions
etc.
Third level consumers
Spiders Shrews Birds
Frogs Bats Predaceous insects
Second level consumers
Birds Miscellaneous herbivores
Grazing mammals Rodents Rabbits Insects
Mites Nematodes Tadpoles
First level consumers
Mosses Lichens Liverworts Ferns Grasses Herbs
Trees Shrubs Algae
Producers

Fig. 4-2 The biotic pyramid. See discussion in text.

All other organisms are, in one way or another, *consumers.* Those which live on vegetation are first-level consumers, predators are second-level consumers, parasites on predators are third-level consumers, and so on. More or less outside the pyramid, but important to it, are the *decomposers,* bacteria, fungi, and the like. They play an important role in breaking down the unused organic matter, so that its component chemicals are returned to the system (see discussion of mineral cycles on p. 82).

A second important point demonstrated by the biotic pyramid is the importance of a broad base. In point of fact, the diagram in Fig. 4-1 is misleading in that the slope is too steep. A more accurate one might look more nearly like this:



It should be emphasized that the broad base represents *biomass* rather than actual numbers. Thousands of tiny leaf-eating insects may feed on one tree; the number of soil mites may reach more than 5,000 per square foot in the first inch of soil (Eaton and Chandler, 1942). Similarly, a second-level consumer like the fox may be a host to a fauna of thousands of fleas, ticks, roundworms, and intestinal protozoa. In terms of biomass, however, the base must always be broader than the higher levels.

The importance of this broad base is evident. If any event in the community reduces the amount of available vegetation (which happens annually in the colder parts of the world), the animals dependent upon it are endangered. Conversely, if the first-level consumers become too numerous, they may deplete the vegetation upon which they depend. Thus thousands of deer starve each winter in the northern states and Canada because of a shortage of available browse. When this happens, the predatory animals, too, are threatened, unless they can survive upon the bodies of the dead herbivores or move to better hunting grounds or change their diet to some more readily available food.

FOOD CHAINS AND FOOD WEBS

The biotic pyramid, of course, is only a rough approximation of the true situation in nature, designed to point out the facts we have mentioned. It ignores other basic facts. For example, some animals may move from level to level. Tadpoles are herbivorous; adult frogs are predators. Bears, as well as human beings, are essentially omnivorous and may feed on organisms of any level. Further, the pyramid implies simplicity where a great deal of complexity exists. In a natural community, hundreds of species are tangled into an inextricable network of eating and being eaten. To trace the flow of energy from level to level, biologists sometimes study the organisms which make up a food chain (Fig. 4-3).

A food chain is really a small part of the biotic pyramid, extracted so that we can study it. Of course such a simple chain rarely, if ever, occurs in nature. Seldom does a single plant species support a single herbivore species which in turn supports a single predatory species. But in each community there are certain basic food chains which carry the bulk of the energy flow, so the concept is a useful one to work with. We shall discuss later a study of one such food chain, which shows energy flow through an old-field community.

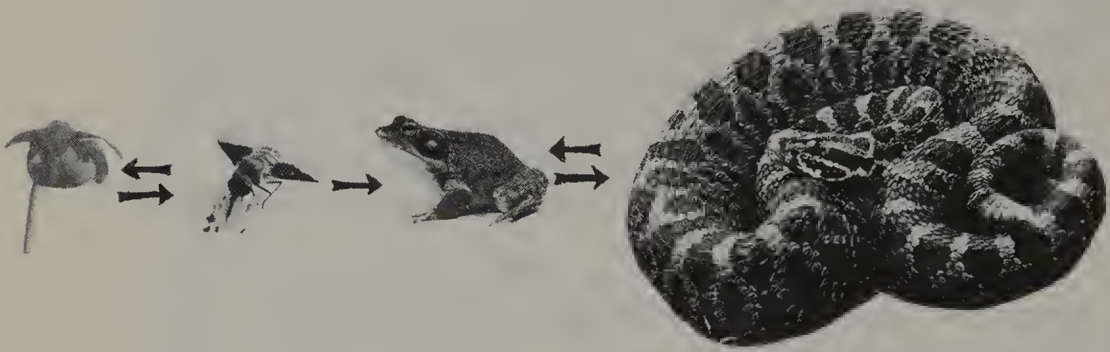


Fig. 4-3 A food chain which occurs in the bog community. This food chain demonstrates how organisms may change places in the biotic pyramid. The pitcher plant may be eaten by insects, but it also eats insects. Adult frogs may eat small snakes, although snakes are major predators of frogs.

Even food chains are artificial simplifications of the real situation in nature. If we could put together all of the food chains in any community, we would have a *food web* (Fig. 4-4). This is merely a complex of food chains with no indication of the degree of importance of each link. It is difficult to construct such a web accurately, for we still are not certain of all of the trophic relationships of even the best-known communities. In terms of energy flow, we cannot even begin to put actual figures into the gaps in the food web. We can guess at values, but we have no precise data for most of these transfers of energy. The food web is a useful device for expressing trophic relationships in a rough qualitative way, but this is all.

BASIC FACTS OF ENERGY FLOW

Modern biologists, however, are not satisfied with rough qualitative data. They want numerical facts, and accurate ones, too. Thus, there is much activity today among ecologists to determine the actual amounts of energy involved in the various transfers which take place in nature. Some of the basic figures are already known, and many more can be approximated. Solar energy, for example, can be accurately measured. Gates (1962) reports this figure for the Northern Hemisphere to be about one-quarter of a calorie per square centimeter per minute as an annual average. In the biotic community, this energy is used in the production of biomass, the amount of living matter per unit area. One unit of expression of biomass is the *standing crop,* the amount of vegetation produced above ground, calculated in grams of dry weight per unit area. Standing crop is easily measured and has an obvious relation to the efficiency with which the community uses the solar energy which strikes it. Getz (1960) found that the standing crop for an old-field habitat was less than 200 grams per square meter, while a grass-sedge marsh in the same vicinity produced nearly 500 grams per square meter. Not only was the marsh more efficient in production, but it also was able to support a greater number of consumers per unit area.

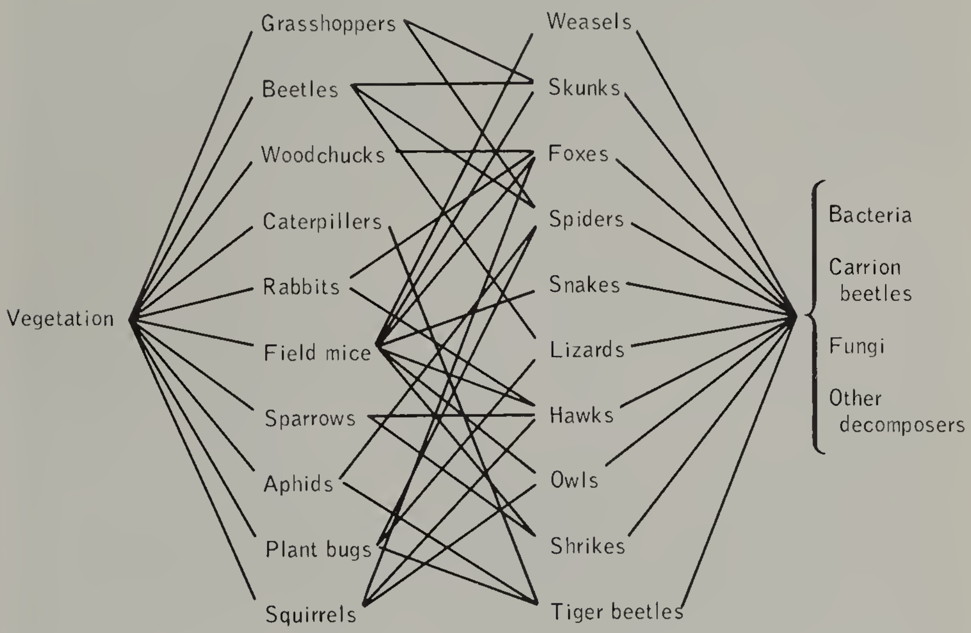


Fig. 4-4 A food web which occurs in an old-field community. Even this complex web is only a partial account of energy interchange.

At the consumer level, it is possible to feed measured amounts of various foodstuffs to experimental animals and to measure losses through organic wastes, respiration, and radiation, as well as gain in biomass. Such measurements were made many years ago with domestic animals, but their application to wild animals is more recent, and many species have not yet been subjected to such experiments. The techniques, however, are available and well known.

The importance of the exchange of energy in an organic community was recognized by many early ecologists. Transeau (1926) attempted to estimate the rate of energy used by plants despite the lack of adequate techniques at that time. Lindeman (1942) proposed that the biotic pyramid ought to be considered in terms of energy dynamics, and he applied his ideas to food chains in fresh-water lakes. Numerous studies have been made on the efficiency of photosynthetic activity, and students of animal husbandry have made numerous studies of the nutritional value of various foods of domestic animals. The groundwork was thus laid for rapid advancement as soon as adequate techniques were available. In the past few years, many students of ecology, particularly Eugene Odum and his students at the University of Georgia, have tried to develop a unified field and laboratory approach to energy field problems. The kind of data which could be obtained and the difficulties still met with were brought out very well in a paper by Golley (1960). In an old-field community in Michigan, Golley found that least weasels (*Mustela rixosa*) were the only significant mammalian predators, the field mouse (*Microtus pennsylvanicus*) the most important first-level consumer, and various grasses the producers. This simple food chain permitted Golley to trace the energy flow through the community with a reasonable degree of accuracy. Figure 4-5 shows the way in which energy flows through this food chain and the losses at each level. As energy passes from one link to the next in the food chain, most of the energy which enters that level is lost. Using this study as an example, we can examine the energy flow as it goes from the sun to the predator.

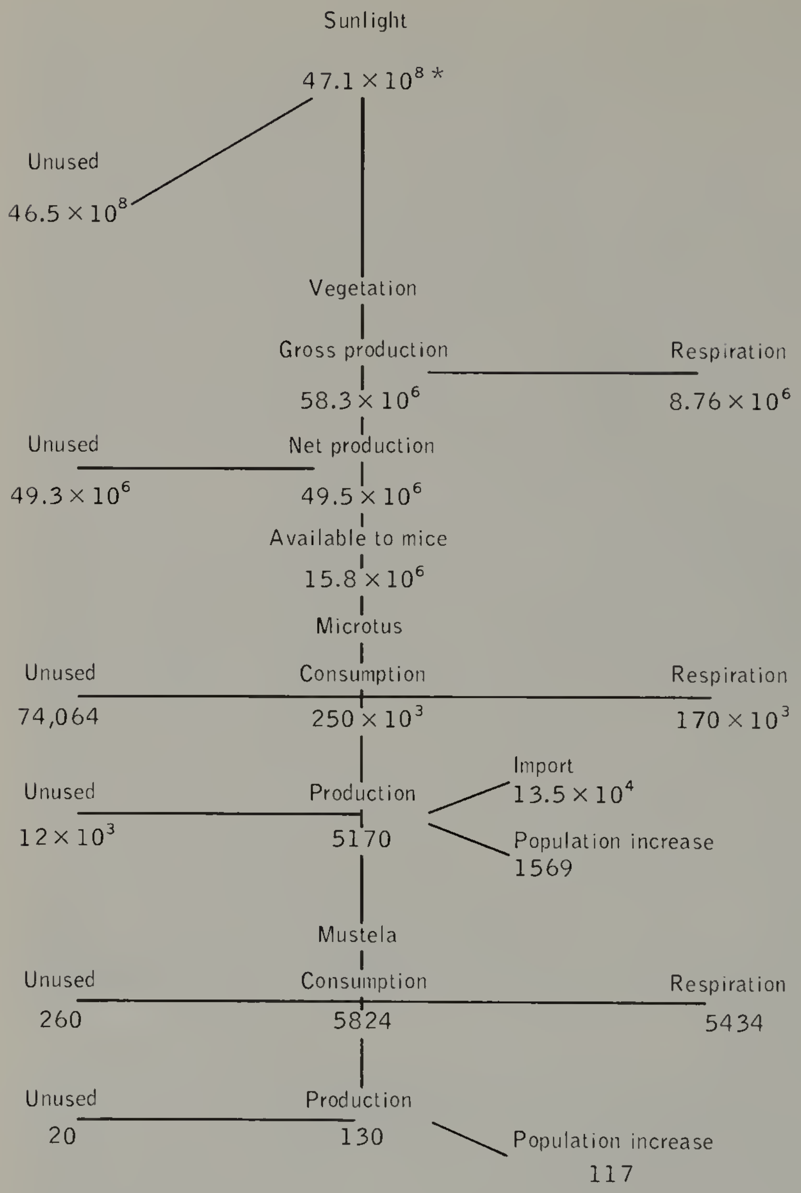
In point of fact, the energy loss begins before the sunlight reaches the earth's surface. That portion of solar energy which is headed toward the earth first enters the earth's atmosphere, where a large portion of the energy is intercepted. This interception is important to life on earth, however, since the ultraviolet rays which would destroy organisms are thus removed from the sunlight.

Of the energy which finally reaches the earth, by far the greater portion is radiated back into the atmosphere. An important aspect of the earth's atmosphere, however, reduces this loss greatly. When the light waves strike the earth, their wave length is changed, and they are radiated back largely as heat rays. These rays do not penetrate the atmosphere so readily and are trapped near the surface of the earth. Because this process is similar to the trapping of heat within a greenhouse, it is spoken of as the "greenhouse effect." Its effect on natural biological processes is very great because the whole atmosphere is thus warmed. Since the Industrial Revolution, man has been increasing this effect by burning vast quantities of fuel, which adds carbon dioxide to the air and increases the effectiveness of the atmosphere in trapping the heat rays reflected from the earth.

Nonetheless, a good bit of energy is lost to the outer atmosphere, never to be regained. In accordance with the second law of thermodynamics, there is a further loss when the solar energy is transformed by green plants into usable energy-producing materials. The theoretical efficiency of this step is a good deal higher than the usual level of efficiency in nature. In a test tube, a culture of a green alga, *Chlorella*, may show an efficiency of up to 20 per cent, but actual production of carbohydrates under field conditions will generally show an efficiency more nearly on the order of 0.5 to 1 per cent. Thus in the diagram of energy flow through the old-field community (Fig. 4-5), the efficiency of photosynthesis was calculated at about 1 per cent.

When this plant material is eaten by a herbivore, there is another large loss of energy. The net efficiency of conversion of carbohydrates into protein may reach about 1 to 3 per cent. However, herbivores generally utilize a rather low percentage of available plant material (Odum et al., 1962), so that loss through waste occurs at this point. In Fig. 4-5, field mice used the vegetation with an efficiency of about 2 per cent, but they consumed only about 2 per cent of the food available.

The transfer of prey protein to predator protein is the last step in this particular chain, and in this case the least weasels demonstrated about 2.5 per cent efficiency, although they showed much greater efficiency in using the available food, consuming about 30 per cent of the available mice. Maynard (1954) indicates that the transformation of one form of flesh into another kind of flesh is usually more efficient, reaching as high as 20 per cent.



*Figures are in calories

Fig. 4-5 Energy flow through a food chain in an old-field community in Michigan. From Golley (1960).

The efficiency of the total operation, from solar energy to weasel, was thus only about 0.000005, disregarding the large amounts of unused but available food. Much of the lost energy went into respiration. The plants used about 15 per cent of the energy in this manner, the mice lost 68 per cent, while the weasels utilized 93 per cent. If additional studies bear out these figures, it will indicate an important difference in maintenance cost at the different trophic levels.

Considering the number of steps at which errors may occur, these figures are, of course, rather rough approximations. In addition, the measurements of ingestion and respiration were made in the laboratory, and extrapolations were made to approximate natural conditions. The techniques of calculating energy flow are worthy of brief consideration, however inadequate they may be at present.

The amount of solar energy, as we have said, has been calculated at about one-quarter of a calorie per square centimeter per minute for the Northern Hemisphere. Variations from this can be calculated from the records of nearby weather stations, so that this figure is probably quite accurate. The production of vegetation is measured by taking a small sample plot, or several of them, and removing all vegetation (i.e., sampling the standing crop of a portion of the study area). This plant material is then dried and weighed, and its caloric content determined by the use of a calorimeter. These techniques are precise enough, providing the sample is both adequate and representative.

Utilization of energy in metabolism by the organisms must be measured, and for purposes of precision this must be done in the laboratory. This problem is pointed up by the work of Odum et al. (1962). They attempted to determine the energy flow through three different types of first-level consumers: the savannah sparrow (*Passerculus sandwichensis*), the old-field mouse (*Peromyscus polionotus*), and a group of plant-feeding Orthoptera. In evaluating the reliability of their results, they suggested that the weakest data were those on respiration. Generally, in such studies, animals are fed in captivity and are then tested with some form of respirometer. The assumption must then be made that the results are similar to those which would be obtained had the animals been free-living. This assumption, as Odum et al. pointed out, is certainly open to question. New techniques for direct measurement of metabolic activities under field conditions are urgently needed.

The degree of error which may occur through all of the measurements, calculations, and assumptions involved in these studies is unknown. Certainly, there is room for considerable improvement in the techniques. But the flow of energy must also be measured in terms of the numbers and biomass of individual organisms. Thus the determination of animal populations and their fluctuations during the period of study is also a source of error. Modern techniques, however, provide something like 95 per cent accuracy in calculating population level, and this is probably more accurate than most of the other approximations which are involved.

Notwithstanding all the sources of possible error, the studies of energy flow in biotic communities give important insight into natural processes. From the purely economic viewpoint, the studies of cultivated plants and domesticated animals are most significant since they represent a food chain to which man is directly connected. Perhaps we are not intimately concerned with a food chain of grass → field mouse → weasel. Still, knowledge of the efficiency of natural processes is basic to an understanding of community dynamics. The generalization of Hairston et al. (1960) that higher-level consumers are more likely to suffer from food shortages than are herbivores is supported by Odum et al. (1962). They found that this is true even within plant-feeding forms, for the seed-eaters used up a much larger percentage of the available food than did the foliage-eaters. Thus we might consider seed-eaters as representing an intermediate trophic level between herbivores (in the strict sense) and carnivores. As the precision of such studies is improved, we can expect to understand both actual and potential energy relations much more fully than at present.

In view of the increasing interest in aquatic communities as sources of human food, the energy flow in such environments is a matter of deep concern. The basic pattern, of course, is much the same as in terrestrial communities, but there are some interesting variations. For one thing, the sunlight that reaches aquatic plants must first pass through water as well as through the atmosphere. Thus the turbidity of the water determines both the depth to which plant life can exist and the efficiency of production of those near the surface. Odum (1957) reported an efficiency of 1.2 per cent for a fresh-water spring, while Lindeman (1941) found an efficiency of only 0.1 per cent for a bog lake with organic matter and dissolved chemicals. Numerous studies of aquatic communities have shown that intensively cultivated fish ponds may produce protein at a rate similar to that of intensively cultivated land, but that the usual rate in natural aquatic communities is much lower. There are some exceptions. Coral reefs, for example, have a very high rate of productivity. Odum (1963) indicates a productivity of 10 to 20 grams of dry matter per square meter per day as the usual range for both intensive agriculture and highly productive natural communities.

Another factor which affects the productivity of any community is the rate of decomposition and re-use of dead organic material. One reason for the immense productivity of tropical rain forests, coral reefs, and certain parts of the ocean is the fact that decomposition goes on at a rapid rate, and material not used as living matter is quickly made available as fertilizer. Olson (1963) found the decomposition of organic matter in tropical forests to proceed several hundred times more efficiently than in northern subalpine forests. Northern forests thus build up a greater accumulation of partially decomposed material, and much more of this material is mixed with the developing soil. Thus the "second-hand" energy of decaying organic matter affects not only the immediate productivity of a community but such basic and long-lasting characteristics as the type, the pH, and the organic content of the soil.

The study of energy flow begins with an attempt to understand simple food chains, but the long-range purpose is much more ambitious. As expressed by McNab (1963), "If we have the proper information on the population of which the individuals are members, then we can construct an energy budget for the entire population. By such synthetic means we can build from the energy budgets of individuals to those of populations and to those of communities; the ultimate goal is to account for all the energy exchange that occurs in a community."

To reach such a goal is obviously going to require a great deal of refinement of techniques, a great deal of reevaluation of data, and the continued efforts of a large number of ecologists both in field and laboratory. Despite the limitations of current knowledge, however, the general patterns of energy transfer are clear and the efficiency at the various levels is already closely calculated. Inevitably this aspect of ecology will be a rapidly developing one for the next few years.

MINERAL CYCLES IN NATURAL POPULATIONS

Some years ago, biology professors used to teach their students about the mythical C. Hopkins, Cafe Mg. This very useful gentleman represented the symbols of the essential elements of protoplasm and was a great help to lazy students. With the recognition, however, of the importance of such trace elements as zinc, boron, cobalt, and molybdenum, etc., Mr. Hopkins became obsolete.

The three elements carbon (C), hydrogen (H), and oxygen (O) make up the bulk of protoplasm and all of the carbohydrates we have mentioned as transferring much of the energy through the population. Nitrogen (N) is a component of the proteins of living things and is also a part of the energy chain. The rest of the elements are present in smaller quantities, but are essential to the function of organisms.

Some of these mineral elements, e.g., phosphorus, potassium, calcium, and magnesium, are present in larger amounts. Sulfur, sodium, and chlorine are necessary in moderate amounts in animal bodies, although only sulfur has been shown to be essential for plant growth. In addition, there are a number of trace elements, including the above-mentioned ones, as well as manganese, copper, and iron. Iodine is essential in animal cells, but not in plants. Some other elements occur in protoplasm but are not known to be essential.

The cycles of minerals follow the biotic pyramid and the food chain. Some of them are also secured as dissolved materials in water. When organisms decay, the minerals become a part of the soil, and if they are not again taken up into the biotic community they may be dissolved and carried away in water. In communities lacking in some important nutrient, both the plant and animal populations may suffer. Such human ailments as goiter, and many other malfunctions of organisms, are traceable to shortages of certain minerals. Fortunately, agricultural science has progressed to the point where such shortages can be readily recognized and the missing elements added in fertilizer. The effects of these deficiencies on natural populations are less easily recognized, and indeed the whole pattern of mineral cycles is only generally known. Undoubtedly a field of great importance, it has been greatly affected by the development of radioactive tracers and is another of those branches of biology in which new techniques hold promise of rapid advances in areas where progress has heretofore been slow.

RADIATION ECOLOGY

Since atomic energy became a common, if often unnerving, aspect of the environment, a new field of bioenergetics has developed. Actually, high-energy radiation of this same type has always been present in nature, but the fallout from atomic bombs and the radiation from radioactive waste have significantly added to its total amount and greatly altered its components.

It was evident from the first atomic blast that this new factor in the environment would have immense biological significance. Research projects were therefore set up at Oak Ridge, Tennessee; Atlanta, Georgia; Brookhaven, New York; and other atomic-project locations. Studies on the biological effects of atomic energy have been pouring out of these laboratories in ever-increasing numbers. Although this increased level of radiation can hardly be considered a normal ecological factor, it has become so important that we can scarcely ignore it in any consideration of energy dynamics.

We must first note that this energy cannot be used to advantage by living beings. Small quantities have the effect of causing mutations at an increased rate. Larger doses are fatal. Different species show startlingly different degrees of resistance, and the fatal level of radiation has been established for many species by studies on bombed areas or in specially devised experimental areas. The amount of radiation at large in the rest of the world is not lethal, except insofar as it may cause harmful mutations.

Radioactive materials enter the biological system by absorption into the roots of plants. Some plants seem to take up such fallout products as strontium 90 selectively and develop high concentrations of this chemical. Strontium 90 has a very long active life and is therefore both especially dangerous and especially easy to trace. After it enters the plants at the bottom of the biotic pyramid, it may be traced to the consumers and on up through food chains to the highest levels. In parts of the Northern Hemisphere, where most of the atomic explosions have occurred, Sr^{90} has reached levels which many biologists think are dangerously high. In short food chains, this radioactive material may reach concentrations which cause some concern both to human beings and to wildlife. It seems that the uptake of Sr is particularly high if the level of calcium in the soil is low, and that abundant calcium reduces the concentration of Sr by vegetation. In animals, Sr may be used in functions normally served by calcium, and appears, for example, in the bones of children by way of pasture grasses, cows, and milk. In the extreme northern regions of the world, Indians and Eskimos are the end organism in a food chain of lichen → reindeer (or caribou) → man. Apparently the small arctic vegetation takes up strontium 90 in large quantities, and this product reaches alarming levels in both caribou and man (Pruitt, 1963). No one is quite sure if the present level is dangerous, or if so, how dangerous, but studies are being continued.

Studies of more severe exposure to radiation have been started at Atlanta and Brookhaven. Woodwell (1963) found that pine trees are extremely sensitive to radiation, being killed by exposures of 20 to 30 roentgens per day. Some herbaceous plants, on the other hand, survived doses of 100 to 300 roentgens per day, the latter dosage being fatal to most of these smaller plants. One plant (*Senecio* sp.) was able to survive even heavier doses, up to 10,000 roentgens per day. The early pioneer plants, mosses and lichens, appear to be even more resistant than herbaceous plants. It is evident that a pine forest, for example, might be reduced to an earlier stage of succession by a relatively small dose of radiation. The levels necessary to produce such a change, however, would occur only in the event of a nuclear war or in the vicinity of atomic blasts.

Most geneticists believe that the most serious results of high levels of radiation will be genetic. A small increase in the mutation rate could lead to serious effects on the population of any species, including man. Relatively little is known about the degree to which present levels of radioactivity might increase the mutation rate, although some predictions have been made by such outstanding scientists as H. L. Muller. At any rate, this is a matter of serious concern, and the whole problem of the effects of radiation is a subject for long-range studies.

There has not yet been time for the completion of such studies, but interim reports have been made. Shields et al. (1963) found that denuded areas on the Nevada test sites have been reinvaded within four years by grasses and other annual plants. Successional characteristics are apparently similar to those on areas of similar biota cleared by less dramatic means. Whether or not long-range studies will show significant changes in response to irradiation must await further study.

In the meantime, radioactive chemicals are proving useful to ecologists as tracers in home-range studies (p. 316), in tracing food chains (Odum, 1963), in studying uptake of minerals in plants and movement of ectoparasites, and in a variety of other aspects of metabolic movement in nature.

The usefulness of radioactive materials appears to be limited only by the ingenuity of biologists, and thus far biologists in both field and laboratory have shown a great deal of ingenuity in adapting these new tools to elucidate old problems. Already radioecology is an established field (see Schultz and Klement, 1963) and one which holds great promise for the future.

Atomic fallout may seem a far cry from Wolstanbury Hill, just as our time seems far from the peaceful existence of Richard Jeffries. But in all and through all runs the same thread of energy, passing from life to life and from level to level, presenting one of the most challenging aspects of study for the field biologist and the laboratory biologist alike.

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chapter 5

Community ecology

An important although limited approach to the study of ecology is the community approach. Ecology is a broad field—the study of the relations of organisms with their environment. Because of the wide scope of this science, it has been divided into smaller fields, including plant and animal ecology and marine and fresh-water ecology. The study of communities approaches the whole field of ecology in a still different manner. It permits the defining of an otherwise clumsily broad topic, yet it does not exclude any group of organisms or any kind of environment. The significance of this approach to ecology is expressed by Clements and Shelford (1939), who state, "Ecology is in large measure the science of community populations."

The word *community* is used in several ways, but in general, it may be defined as all of the organisms that exist as interrelated members in a given area. The size of the community will depend upon the degree of diversity of the environment in a geographical area and the way in which this diver-

Every reflective biologist must know that no living being is self-sufficient, or would be what it is, or would be at all, if it were not part of the natural world. . . . Living things are real things . . . but their reality is in their interrelations with the rest of nature, and not in themselves.

W. K. Brooks *

sity affects the organisms present. Usually, one or more major environmental factors, such as amount of moisture or type of substrate, will define the limitations of a community. A salt-water marsh, for example, can exist only where the substrate contains salty or brackish water. On the other hand, more than salty or brackish water is required for such a community, including certain climatic conditions, depth of water, and bottom type. The plants and animals of a community may be considered separately for convenience, but even early ecologists such as Clements, Adams, Shelford, and others (see Chap. 2) recognized that plants and animals comprising communities are interdependent, forming a single unit. Plants, animals, and their environment as a functional unit constitute an ecosystem. In this chapter we will consider ecosystems of communities of various sizes.

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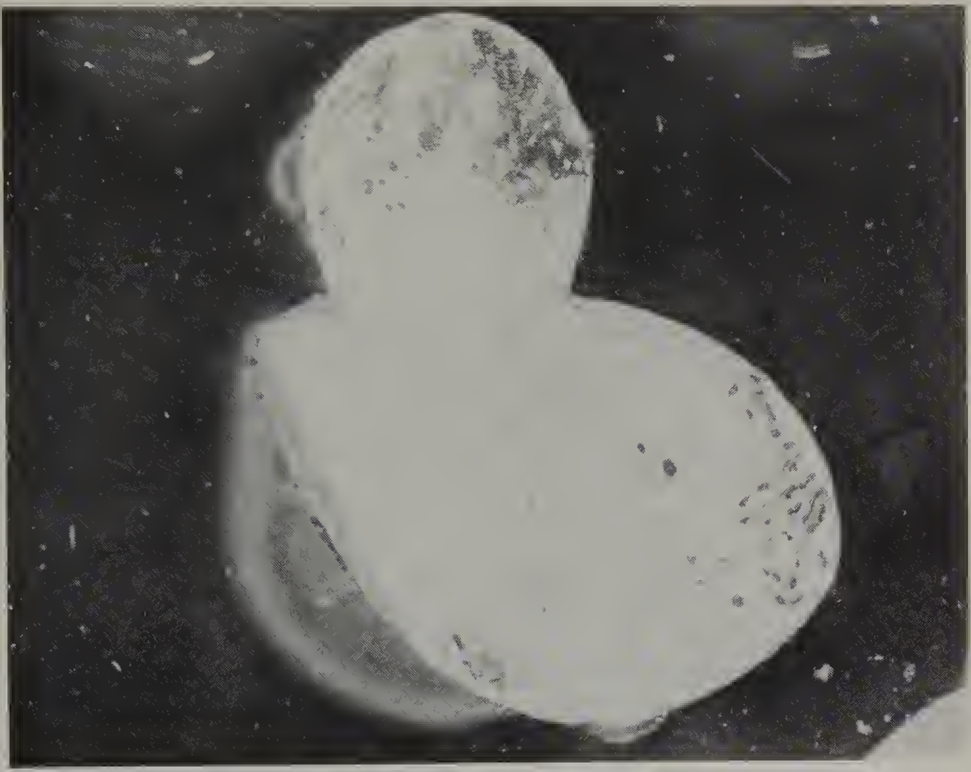
* Heredity and variation: logical and biological. 1906. *Proc. Am. Phil. Soc.*, 45:70–76.

FACTORS AFFECTING COMMUNITY TYPES

Certain environmental conditions may be of prime importance in a community ecosystem. Topography, soil, and various aspects of the climate including rainfall, temperature, growing season, and wind are the more important general physical conditions that may determine what types of plants will exist in a given locality. Since animals ultimately depend on plants for nourishment, plants are an important environmental factor in determining the presence or absence of animal species in a given community. Plants also provide animals with shelter and protection from their enemies or the elements. On the other hand, animals may affect the vegetation of a community. Other significant environmental factors to be considered are fire, snow cover, fog, and the presence of unusual amounts of salts or minerals. Not only do environmental factors affect a community, but a community may affect the environment. This is another way of expressing the concept of the total interrelationship of plants, animals, and the environment—the ecosystem.

Plants

Plants may alter the physical conditions of the environment or by themselves provide an environment. For example, certain plants grow only where sunlight is limited, a condition provided frequently by a canopy of other plants. Trees shading a stream may allow some animals, such as various species of fishes or amphibians, to survive and inhabit the stream because of the resulting cooler temperatures. Plants such as the minute aquatic duck weeds, *Lemna* sp. (Fig. 5-1), may serve as a microcommunity for the tiny insects that mine or eat out the insides of these plants. One worker (Scotland, 1934) found that two species of insects are obliged to live their lives within the thallus of *Lemna minor*. Many other animals are associated with these tiny plants, including occasional residents and their parasites. Forests transpire enormous amounts of water and thus raise the relative humidity of the air. Plants greatly affect the rate of erosion and the water-holding capacity of the soil.



Minnie B. Scotland

Fig. 5-1 A single thallus of *Lemna minor*, a tiny flowering plant about one quarter inch in diameter, which represents one of the smallest microcommunities. Note scars made by feeding of Lemna fly, *Lemnaphila scotlandae*, and egg on edge of leaf at bottom.

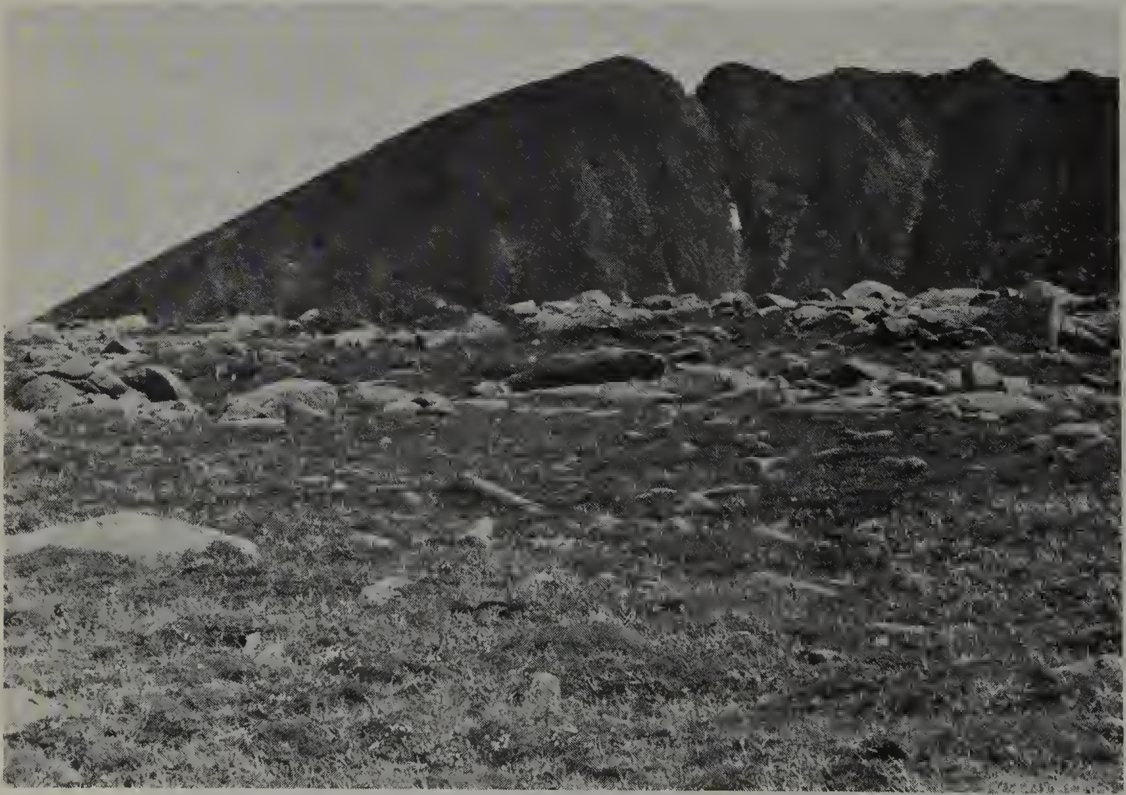
Animals

Some of the effects of animals on the ecosystem may be obvious, whereas others may be inconspicuous yet nonetheless significant. Grazing animals such as cattle may selectively eat certain species of plants and change the plant composition of the community drastically (Figs. 11-4, 11-10). The trampling of large herds of cattle may kill plants and compact the soil. Insects such as the Englemann spruce beetle may kill many individuals of a tree species in a community. Burrowing mammals, worms, insects, and other animals promote aeration and drainage of the soil and help to fertilize the soil. These activities not only affect the rate of erosion but also plant growth. Occasionally, as in bird rookeries, accumulation of fecal material will cause a change in the vegetation of the area, as nitrogenous materials accumulate to excessive amounts on the soil, covering and killing the trees, shrubs, and herbs. The habits of beavers in felling trees and building dams, which flood valleys and destroy vegetation, is another well-known example of the many ways that animals may affect the vegetation, the physical environment, and thus the community as a whole.

General Topography

Within a given area there may be several different kinds of communities, depending on the variation of the habitats. Hilly or mountainous regions are apt to have a wider variety of habitats than flat areas. There is a greater opportunity for variations in moisture, light, and other factors, which consequently produce different communities.

Variation in topography may produce not only minor community differences but major ones as well. Poorly drained areas will have different communities from well-drained areas. North-facing slopes of hills and ravines will be cooler and therefore have slightly different communities of plants and animals than the south-facing slopes. Conversely, plants may



Ralph S. Palmer

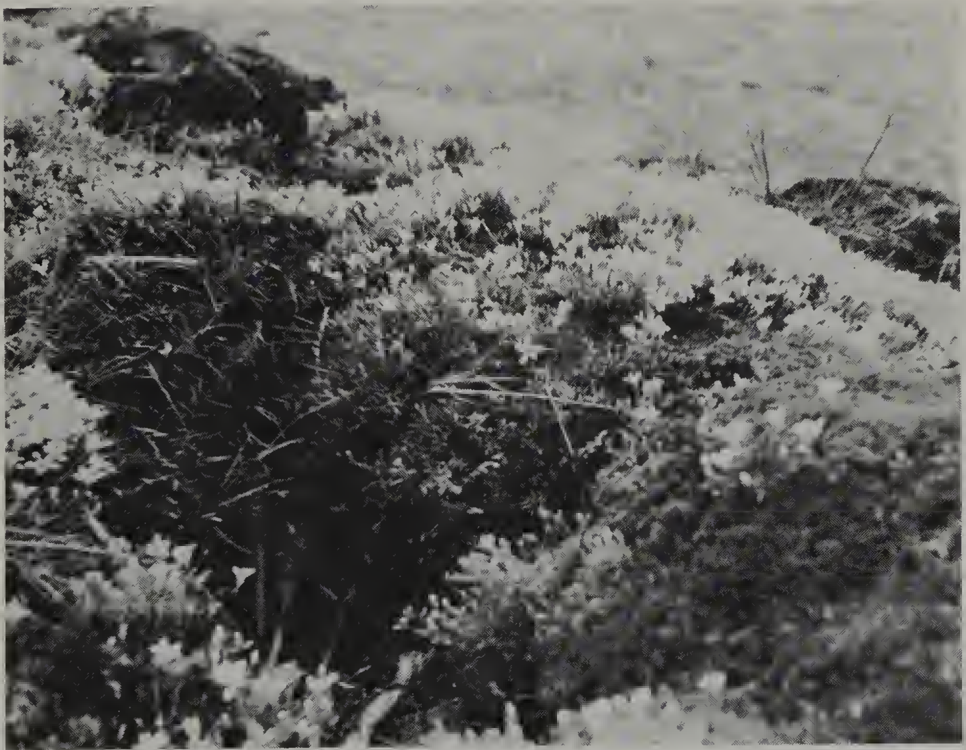
Fig. 5-2 Tundra on a mountaintop. Mt. Katahdin, Maine.

affect topography, as in the stabilization or growth of sand dunes.

Altitude

Elevation may produce great differences in community types. As one ascends a mountain, the temperature drops, the amount of precipitation changes, and in general the environment becomes more rigorous. If a mountain is sufficiently high, these changes due to elevation will be great enough to cause the appearance of several different community types from the bottom to the top of the mountain.

High mountains may be so cold on top and may often have such a rigorous climate as to possess treeless vegetation in a region that is in a generally forested area (Figs. 5-2, 5-3). Such a treeless area is a tundra community type. On Mount Washington, in New Hampshire, the tundra begins at elevations of between 4,500 and 5,700 feet and continues to the top of this mountain, which is only 6,288 feet high (Griggs, 1946). In different latitudes and climates, the elevation at which the



Allen H. Benton

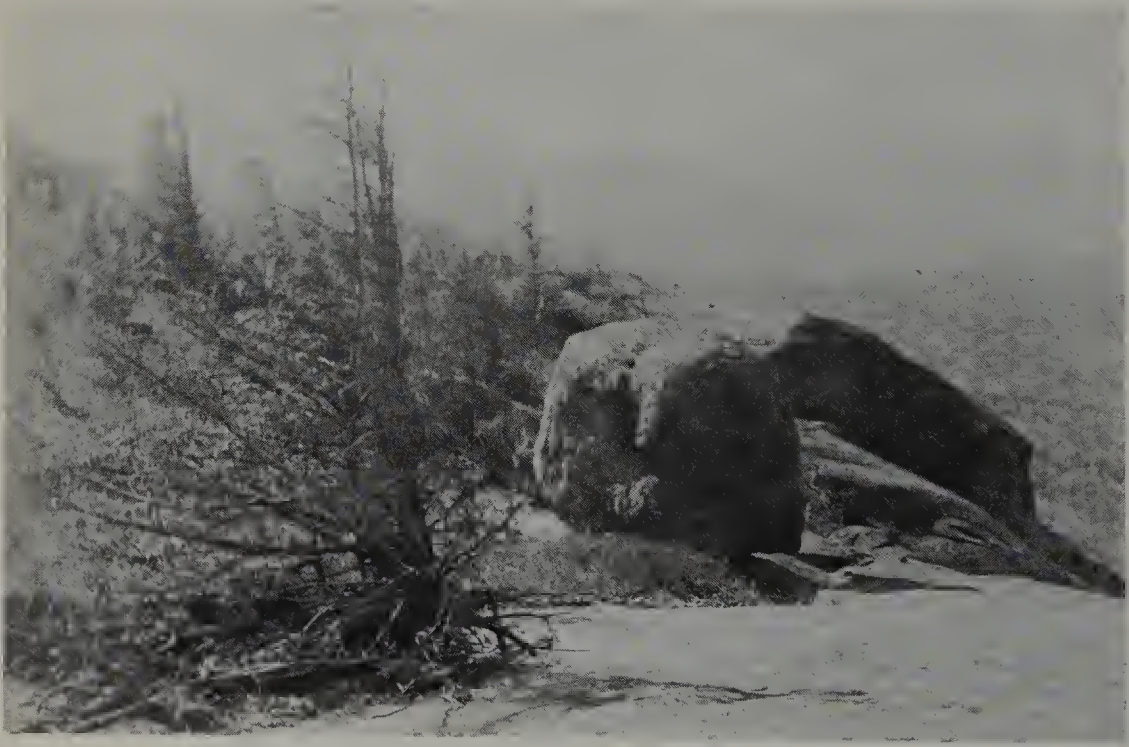
Fig. 5-3 Close-up view of alpine tundra on Whiteface Mountain, New York, at about 4,500 feet.

tundra commences will vary. In the Rocky Mountains, for example, it begins in Montana at about 8,000 feet, and in New Mexico at about 11,500 feet.

Just below the tundra on a mountain is a region of stunted trees, often called the *Krummholz* (Fig. 5-4). Here trees such as balsam fir or spruce invade the tundra area behind the abundant rocks in wet areas. They are not able to grow above the rocks and are so bushy that it is possible to walk on top of them. Where large rocks are absent, these trees are not found.

Below the *Krummholz* will be found a subalpine coniferous forest. Because of lower elevations, the temperatures are not so cold, nor are the winds so severe. In general, the climatic conditions, including increased moisture, are more favorable to growth of trees. This type of community will extend down the mountain until it is replaced by either a deciduous or another coniferous forest community. The altitude at which this transition occurs will again be determined by latitude and general climatic conditions.

At still lower elevations, other communities will be found. The coniferous or deciduous forest replaces the subalpine coniferous forest where the elevations are such that temperatures



Allen H. Benton

Fig. 5-4 . *Krummholz* zone, at top of Pitchoff Mountain, Adirondack Mountains, New York.

are milder and moisture is abundant. If the mountains are in grassland area, the forest will finally give way to grasslands at their base as moisture decreases. In the Southwest, where mountains are in a desert region, one may ascend from desert through a savanna, coniferous forest, subalpine coniferous forest, and finally to tundra. All these community differences are primarily the result of change in temperature and moisture due to change in elevation (Fig. 5-5*a*, *b*, *c*).

Lake-bottom Topography

In aquatic environments, bottom topography may create differences in communities. A deep lake may be quite different in its communities from a shallow lake. A shallow lake has the major portion of its water set in motion by winds rather easily; therefore the water turns over from top to bottom during the summer and warms fairly evenly. In deep lakes the bottom waters are never greatly warmed, and a *thermocline,* or area in which the temperature of the water drops rapidly in a vertical direction, is formed during the summer months (Figs. 7-7, 7-8). While the thermocline lasts, water does not circulate from top to bottom, resulting in such adverse conditions as depletion of nutrients at the surface and depletion of oxygen and accumulation of undesirable products at the bottom. During the winter, ice may form on shallow lakes, causing circulation to stop and producing stagnation. Deep lakes will also freeze, but their large volume will contain sufficient oxygen to prevent stagnation. A shallow lake may support much more vegetation and in general be more productive, owing in part to the summer circulation. Another important factor is that in a shallow lake a larger percentage of shallow water permits more rooted aquatics to grow, which of course provides food for more animals. Depth of water also has its effect on the types of communities found in streams, often through the factors of oxygen and light.

Climate

A prime factor determining community types is the climate. The climate, in large degree, controls the rate of topography changes. It is important in determining vegetation type and associated animal life in any area. It is involved in the control of the development of the soil and the rate of repopulation and development of communities in which life has been destroyed.

Climate affects the rate of topography change through rainfall, temperature, and wind. Increased rain ordinarily means increased erosion, although vegetation may well restrict this action in varying degrees. Mountains wear down to plains, and bodies of water fill in or drain mainly as a result of erosion. Wide seasonal changes of temperature producing alternate freezing and thawing cause greater erosion than more uniform temperatures where freezing and thawing are not involved. Also, the presence or absence of strong prevailing winds will vary the amount of erosion by wind in any given area.

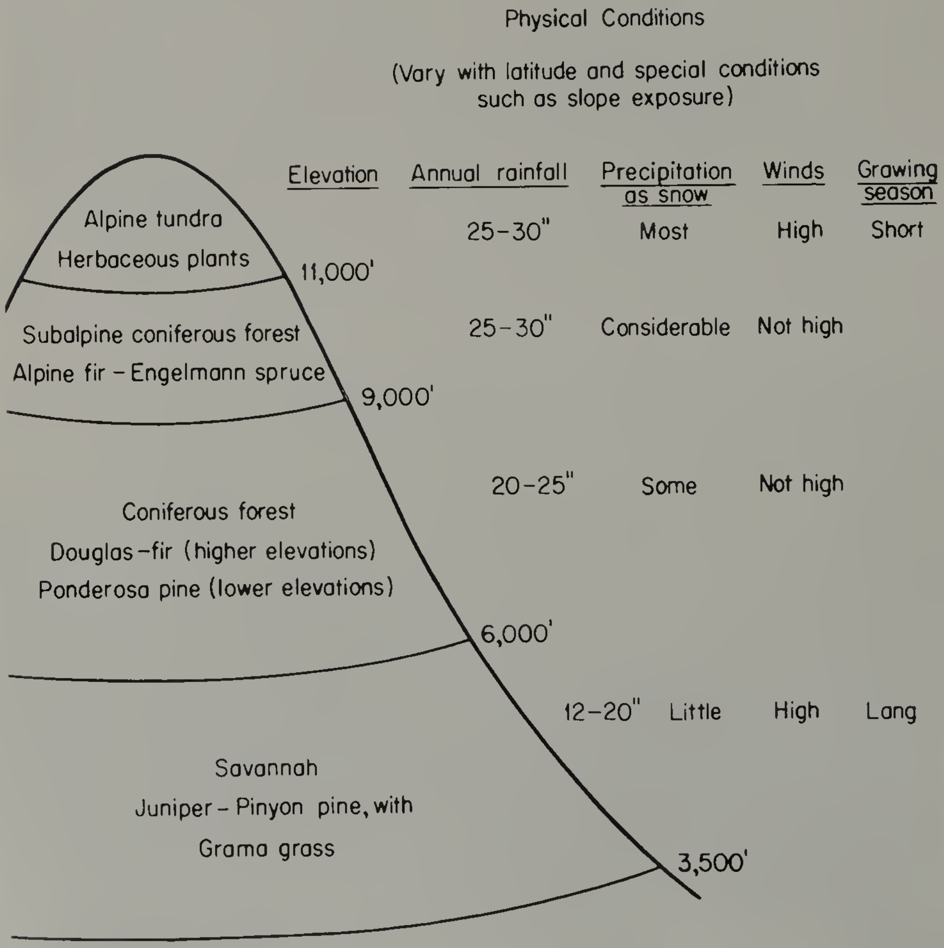
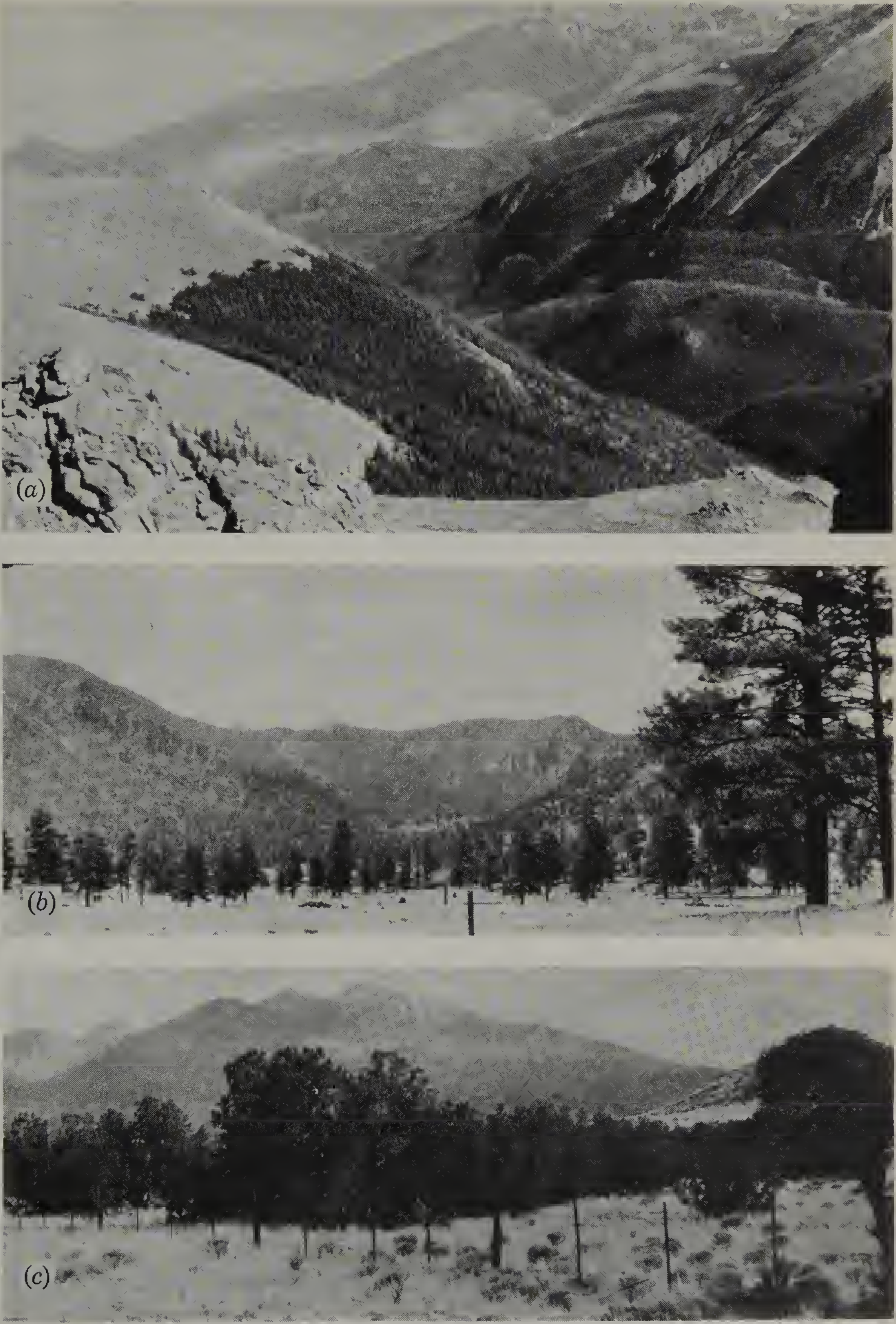


Fig. 5-5 Altitudinal zonation in western United States: above, diagrammatic representation of zones and summary of environmental conditions; right, views of different altitudinal levels; (*a*) Alpine tundra and spruce-fir coniferous forest in Rocky Mountain National Park, Colorado; timber line is at about 11,500-foot elevation; (*b*) Pine coniferous forest; ponderosa pine, *Pinus ponderosa*, near Flagstaff, Arizona, at about 7,000-feet elevation; (*c*) Juniper-pinyon pine savanna, near Flagstaff, Arizona, at about 5,000-feet elevation.


(a)
(b)
(c)

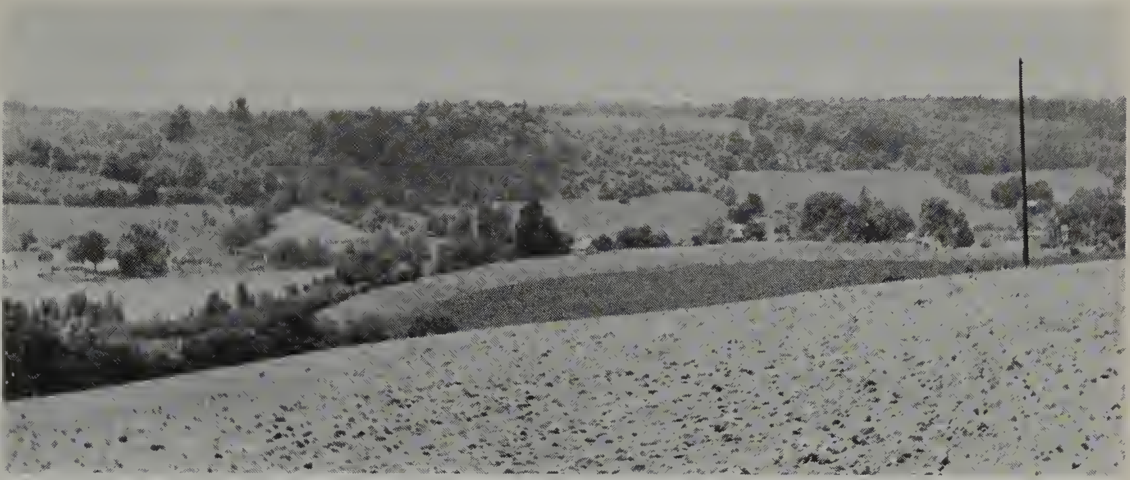
Plants are dependent on several factors of the climate, principal among which are rainfall, wind, temperature, and growing season. The first three are closely related, for wind and temperature may control the amount of water evaporated from the soil and thus made unavailable to plants. Areas of high rainfall and relatively low evaporation rates, such as tropical rain forests, have a different vegetation from that of areas of low rainfall and high evaporation rates, such as deserts. The length of the frost-free part of the year (growing season) is frequently of importance in controlling the distribution of plants and hence community types, for some plants require a longer period for growth and reproduction than others. The plants present often determine what animals are present, and thus the climate affects a whole community. (See the discussion of climax communities and biomes below.) If the organisms of an area are destroyed, the rate at which they will grow back will be influenced by the amount of rain, light, wind, and other factors of the climate.

Soil

The type of parent rock or soil on which a community is found may markedly affect its development and composition. In deserts, for example, volcanic rocks and granitic rocks may exist in the same climatic area and will be occupied by different communities. Agents of soil transportation such as glaciers, wind, and rivers may deposit soils of varying textures such as silt, clay, sand, gravel, or rocks over bedrock. The physical differences of these materials may directly or indirectly restrict the type of plants and hence the entire community that may grow on them. Thus sand allows excessive drainage or evaporation, tending to produce xeric conditions, while clay may hold water and permit development of a wet situation. In general, soil having fine particles tends to hold water and certain minerals well, but may also compact when dry. Soil having coarser particles does not hold water as well and does not compact as much when dry.

TYPES OF COMMUNITIES

A major division of types of communities is between land (terrestrial) communities and water (aquatic) communities. Land communities include such varying habitats as areas recently denuded of life, rocky areas, meadows or grasslands, and



Allen H. Benton

Fig. 5-6 A variety of communities and agricultural land in central New York. Secondary successional stages can be clearly seen on the distant hillside.

forests (Fig. 5-6). Slow streams, fast streams, ponds, bogs, swamps, and lakes comprise some of the broader types of aquatic communities (Fig. 5-7).

The Microcommunity

Within each of these divisions may be smaller communities, such as an oak-hickory forest, or the forest floor litter of such a forest community. The latter is an example of a community type or microcommunity and is in reality a specialized community dependent on the larger community of which it is a part.

Microcommunities are often convenient to study, owing to their size and easier definition. One can study the community of plants and animals of a fallen log in an oak-hickory forest, momentarily neglecting the total ecology of the forest community, although the forest community is a part of the log community and vice versa. Similarly, one could study the community of plants and animals in pebbles at the edge of a lake, momentarily neglecting the total ecology of the lake of which the smaller community is a part. Yet neither of these smaller units could exist or be completely studied outside the context of their natural surroundings. A log exposed to the sun in an open field would not have the same inhabitants as one in a damp, shaded forest, and pebbles at the shore of a

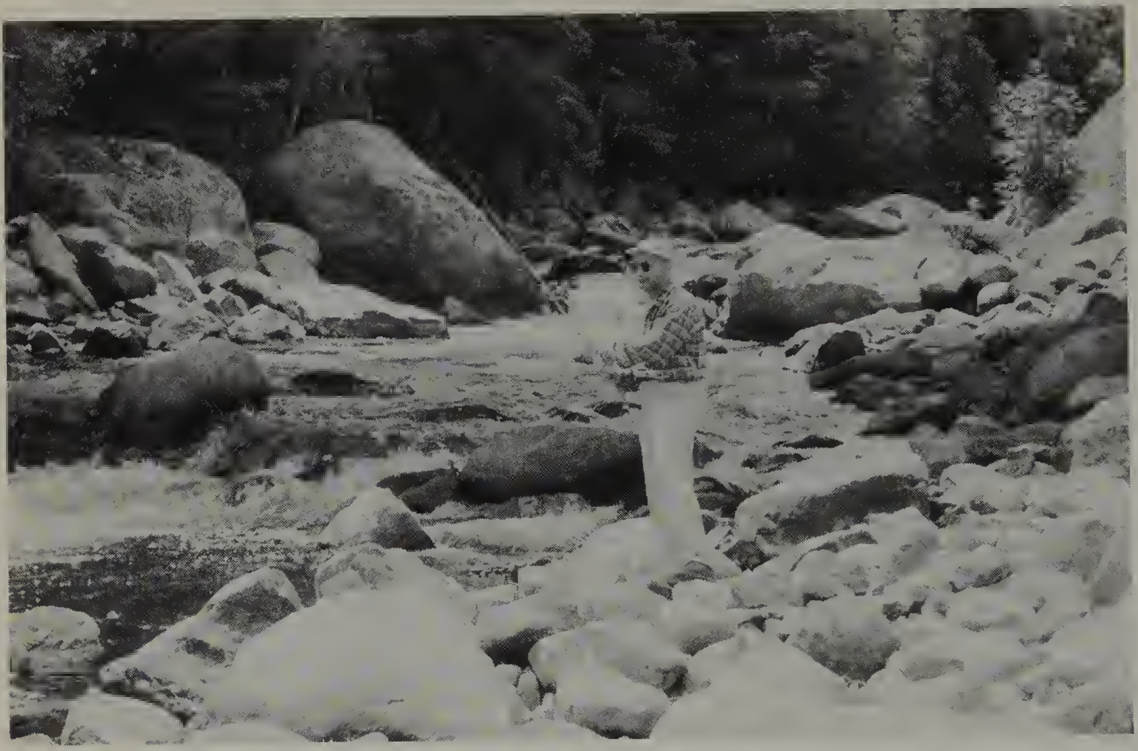


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Fig. 5-7 A fast-stream community, the Ausable River, a famous trout stream in the Adirondack Mountains, New York.

beach will encourage life vastly different from life surrounding pebbles of a dry gravel bank far inland.

Climax Communities

Geography and geology teach us that eventually mountains wear down to hills, and hills to plains. Deep lakes fill in and become shallow, passing then into ponds, swamps, and finally dry land. The type of soil may change because of the continual processing by the organisms living in and on it, from accumulation of organic matter, and from leaching or lack of leaching. These changes are a part of a process called succession, which will be discussed later (see Chaps. 6 and 7).

Changes in topography are going on continually, but in most areas a relatively stable condition is eventually reached. The controlling elements of this stable condition include the climate of the area, interaction of plants and animals, and other conditions. For example, rainfall and wind may hasten erosion, while vegetative cover and small burrowing animals may help prevent run-off and erosion. When the topography is more or less stabilized, the plants and animals of the area may reach a steady state also.

A community which maintains a marked degree of stability is called a *climax* community. Although there may be changes in species composition over a period of time, in general such changes will be minor and will tend to be of an oscillating nature. The accidental nature of dispersal of seeds of the plants, the disruptive effects of hurricanes, insect injury, or disease may allow one species to become more numerous than it was formerly, another species to become less abundant. With time, such shifts may reverse, but in any case these changes are not directive, and the community will remain essentially the same. (See Chap. 6 for a fuller discussion of climax.)

Minor variations in biotic and physical factors may produce minor variations in climax communities. For instance, along the Hudson River Valley in New York State is found a climax type in which oak and hickory are dominant trees. That is, these trees are the controlling and characteristic species of the community. Slightly to the north, continuing west in New York, is the Mohawk River Valley, where the climax includes such dominants as beech, maple, birch, and basswood. Both types of climax communities are deciduous types as far as dominants go, although some conifers such as white pine and hemlock may be found in the area. The slight difference in climax type is due to slight differences in climate and other environmental factors.

Successional Communities

In many places the major community type is not a climax community, nor is it in any sense stable. It is characterized by continual and marked shifting of the constituent species, allowing a gradual evolution of the community toward the climax community. Such a community occurs in areas where organisms have been severely disturbed by man or nature, as in a region where life has been destroyed by fire or bulldozers. In these areas communities will grow back toward the climax community. Communities that are in the process of growing back are called successional or seral communities. A *sere* is a sequence of developmental communities leading to the climax of an area.

LIFE ZONES

It is not too surprising to find that one of the earlier attempts to classify communities was a result of the observations of the distinctive mountain zonation of the West. The naturalist C. Hart Merriam devised the "life zone" concept in which temperature was the most important factor determining the distribution of plant and animal species. His life zones—tropical, lower Austral, upper Austral, transitional, Canadian, Hudsonian, and arctic—followed isotherms closely and were in sequence from the tropics to the arctic and from bottom to top of mountains (Merriam, 1898). Merriam's zones did not always fit the distribution of plants and animals, especially in that the zones were transcontinental, while major communities are not. The zones also presupposed certain faunal origins which since have been shown to be incorrect.

BIOTIC PROVINCES

Another system of classification of communities is according to units called biotic provinces. A biotic province is a large, continuous area in which the climate, physiography, and soil type are relatively uniform, and in which there is one or more ecological associations that differ from adjacent provinces (Dice, 1943). Although the system is a useful one for certain biologists, it is based primarily on the distribution of animals, rather than plants and animals.

BIOMES

A third system of classification of larger communities is according to units called *biomes*. Each biome (or biotic formation) is an ecosystem of a large area in which the climax communities are similar in appearance. A given biome, however, includes not only climax communities but successional ones as well. The area included in one biome is large and may not be continuous. For example, the coniferous forest biome is found on the higher mountains of the East and West, as well as in a band across Canada. The coniferous forests of the mountaintops and Canada are not all joined together. So it is with most of the biomes. This is an essential difference from biotic provinces. Plant and animal species may not be the same in the discontinuous and main parts of the biome.

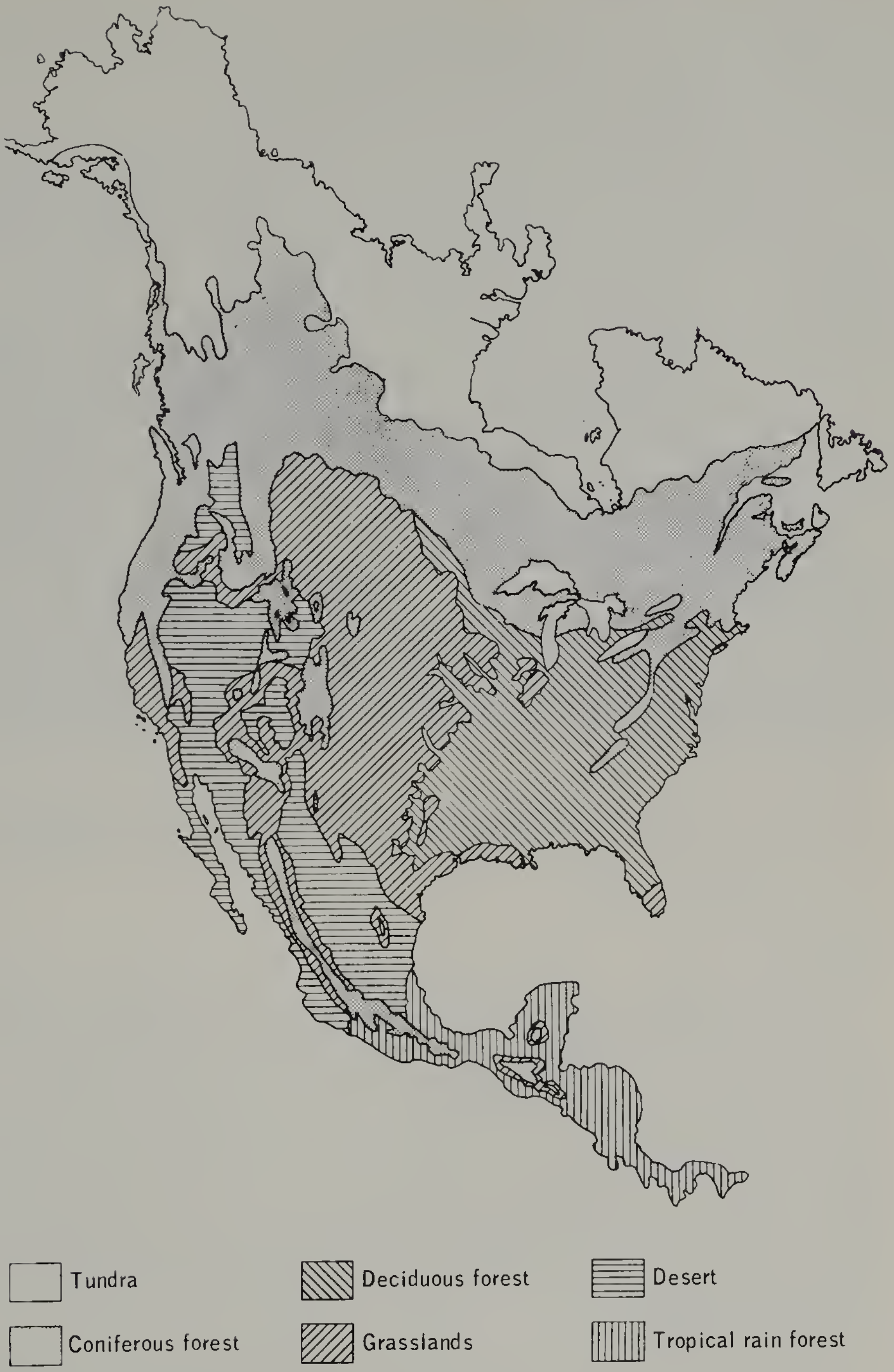


Fig. 5-8 Biomes of North America. *Map adapted by permission of Frank A. Pitelka, American Midland Naturalist,* 25:113–137.

They may be replaced by a similar organism of a taxonomically different species performing a similar ecological function.

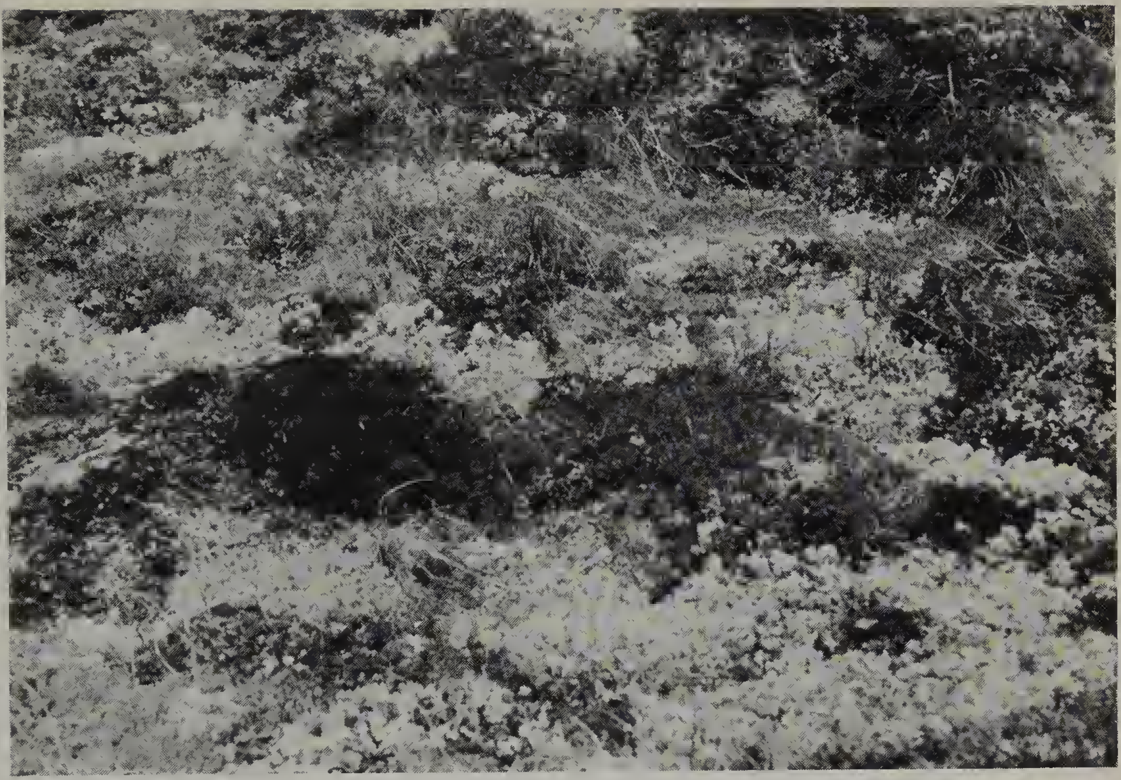
The biome is similar to the *formation* in plant ecology but takes animals as well as plants into consideration. Often there are animals which may inhabit successional communities as well as climax communities and may range over several climax and seral communities of a biome. These animals help to give unity to the biome and make it the fundamental large unit of ecosystems (Shelford, 1932).

The biome is not without its shortcomings as a system of community classification. It is often difficult to determine the boundaries of a biome and even to determine how many biomes there are. Biomes are recognized primarily by the dominant plants of the climax communities, but in many parts of the country communities have been severely disturbed by man. Also, some communities are considered to be transitional between two biomes (*ecotone*) by some ecologists, but because of their large extent may be considered as distinct biomes by others. Subdivisions of the biome become even more difficult to define, for the same reasons. Despite these problems, the system is a useful one and allows an ecosystem approach. In the remainder of this chapter, only the major terrestrial biomes of North America (Fig. 5-8) will be discussed. (For a concise picture of the biomes of the world, see Kendeigh, 1961.)

Tundra

The tundra biome (Fig. 5-9) occurs in the higher latitudes of the north and at sufficiently high elevations elsewhere. The tundra of the north is known as the arctic tundra, while that of the mountaintops is known as alpine tundra. The low tundra is differentiated from the *taiga* biome to the south with some difficulty (Polunin, 1955; Britton, 1957), although the July isotherm of 10° Centigrade is often used. The isotherm of 5° Centigrade is used to mark the line between the high and low arctic tundra.

Several climatic and physical features are responsible for the distinctive nature of the tundra communities. Chief among them are low temperatures and a limited amount of available water. Other important factors are nearly continual winds, permafrost, short growing season, and unstable soil. In the arctic tundra, illumination varies from continual but low intensity during the summer months to continual darkness



Ralph S. Palmer

Fig. 5-9 Close-up of arctic tundra, Churchill, Manitoba. Compare with Fig. 5-3, p. 94.

in the winter. In alpine tundras, thin air permits high amounts of ultraviolet light to reach the surface. Heavy snows (up to 60 feet), low concentration of oxygen, and low barometric pressure are other alpine features.

Temperatures are low during the winter months. At Churchill, Manitoba, −70° Fahrenheit is not uncommon (McClure, 1943), and the minimum temperature observed at Point Barrow, Alaska, was −56° Fahrenheit (Britton, 1957). From June through August, the air temperatures moderate. Daily maximums average in the mid 60s in July at Umiat, Alaska, but reach as high as 85° Fahrenheit. At Churchill, Manitoba, temperatures up to 100° Fahrenheit have been recorded (McClure, 1943). Minimum summer temperatures fall to the 30s. Soil warms up faster each day at the surface, but lags at lower depths compared to the air (Bliss, 1956). Snow or frosts may occur even during the warmest months at Point Barrow, Alaska (Britton, 1957). In alpine tundras, similar temperature ranges occur, although there may be more weekly fluctuations instead of gradually increasing temperatures to midsummer (late July), and gradually decreasing temperatures thereafter.

Summer precipitation is similar in the arctic and alpine tundras, reaching a maximum of 4 to 7 inches. Black (1954) estimates that the annual rainfall at Point Barrow is probably about 16 inches. At Churchill, Manitoba, average precipitation is about 20 inches a year. In winter, much more snow accumulates in the alpine tundra than in the arctic. Drainage in the arctic regions is generally poor, so that numerous ponds and bogs are formed from melting and thawing ice and snow.

Atmospheric moisture is essentially similar in the alpine and arctic tundras, ranging from 100 per cent relative humidity at night to as low as 35 per cent at 1 to 2 P.M. Bliss (1956), comparing Umiat, Alaska, and the Snowy Range of Wyoming, found that the alpine air was somewhat less moist than the arctic. Soil moisture at Umiat was never low enough to be critical for plants, whereas in the alpine study areas, high moisture levels were maintained only in bog areas. In Alaska, because of the high moisture content of the air and the permafrost holding water near the surface, plants in most areas probably are always able to obtain sufficient water during the growing season unless prevented by cold soil temperatures.

Associated with air moisture, of course, is wind, which may dry soils and hasten transpiration from plants. McClure (1943) noted only 96 hours of calm from June 10 to August 2, or 8 per cent of the time. At Churchill, Manitoba, Bliss (1956) noted little adaptation of vegetation to wind in Alaska, but on mountaintops, pruning effects on dwarf shrubs are clearly evident and cushion growth form is more important, also indicating the effect of wind. Thus, both areas are windy, but much stronger winds occur in alpine tundras.

Another feature of tundra is permafrost. In the Alaskan arctic, except in certain spots such as gravel and sand banks along the streams and under the streams themselves, the soil will be frozen during the winter to depths of 800 to 1,200 feet. It will thaw only to relatively shallow depths during the summer, the exact depth of thaw varying with soil type and exposure as well as vegetation type. Thus Bliss (1956) found that vegetation decreased thaw, while greatest thaw occurred on bare soil on south-facing slopes (maximum 32 inches). In the Colorado Rockies, Retzer (1956) found permafrost extending from 60 to 400 feet, with summer thaw varying from

1 to 8 feet. In the Rockies of Wyoming and Montana, Johnson and Billings (1962) found thaw to depths of 1 to 2½ feet.

While permafrost has its restrictive effects on plant and animal life, it is also important in soil formation. Permafrost slows down erosion by winds and streams. Thus these erosive factors are greatest where thawing is maximum, as along streams and shores. Freezing and thawing, with the consequent splitting, heaving, and churning, produces characteristic patterns of polygons, nets, and circles on flat surfaces, and stripes and steps on slopes (Britton, 1957). The instability of the soil makes it probable that plants cannot affect the development of the soil in the usual sense (Polunin, 1955). In alpine regions, the instability of the soil produced by thawing and freezing may be a major factor in defining the limits of the alpine tundra (Johnson and Billings, 1962).

In the arctic, the season for plant growth is limited. On the other hand, during this season day length is greater than at lower latitudes, being continuous from May to late July. Plant growth for some species apparently begins when air and soil temperatures exceed 32° Fahrenheit, whereas others may require warmer air temperatures (Bliss, 1956). Some species show greatest growth during warm spells, although other plant species do not show increased growth under this circumstance, indicating factors other than temperature are involved. Some species end their growth while air and soil temperatures are still high. In alpine tundras, day length is much less during the growing season (depending on latitude) compared to the arctic, and this may have its effects on growth, flowering, and fall dormancy.

Many of the plants and animals of the arctic tundra are circumpolar, but alpine tundras tend to have relatively few species (about 30 per cent) in common with the arctic. Due to the isolation of mountaintops, there are many endemic species in alpine tundras (Fig. 5-3). On high mountains and in the far north, regions of perpetual ice and snow are found where vegetation is nearly absent and a virtual alpine or polar desert exists.

The vegetation of the tundra is far from uniform or simple in organization, perhaps because of the youth and instability of the soil. Freezing and thawing continually disrupt plant communities. Furthermore, much of the area has recently been glaciated, while other areas have just emerged from the sea. Thus, plant communities are in a state of flux.

Certain vegetational features are distinctive, however. Large woody plants are absent, although dwarf forms of trees (e.g., willows) and decumbent shrubs are found. In any event, non-woody plants usually dominate, especially lichens and mosses. Despite the rigorous conditions, a surprising variety of plants succeed in the tundra. Polunin (1955) has totaled 900 species of plants that have been collected in the arctic tundras of the world. Churchill (1955) classified vegetation in the Umiat, Alaska, area into five major categories: (1) dwarf-shrub heath type, (2) frost-scar collective type, (3) willow type, (4) alder type, and (5) sedge-marsh type. Each of these major types was further subdivided into minor ones.

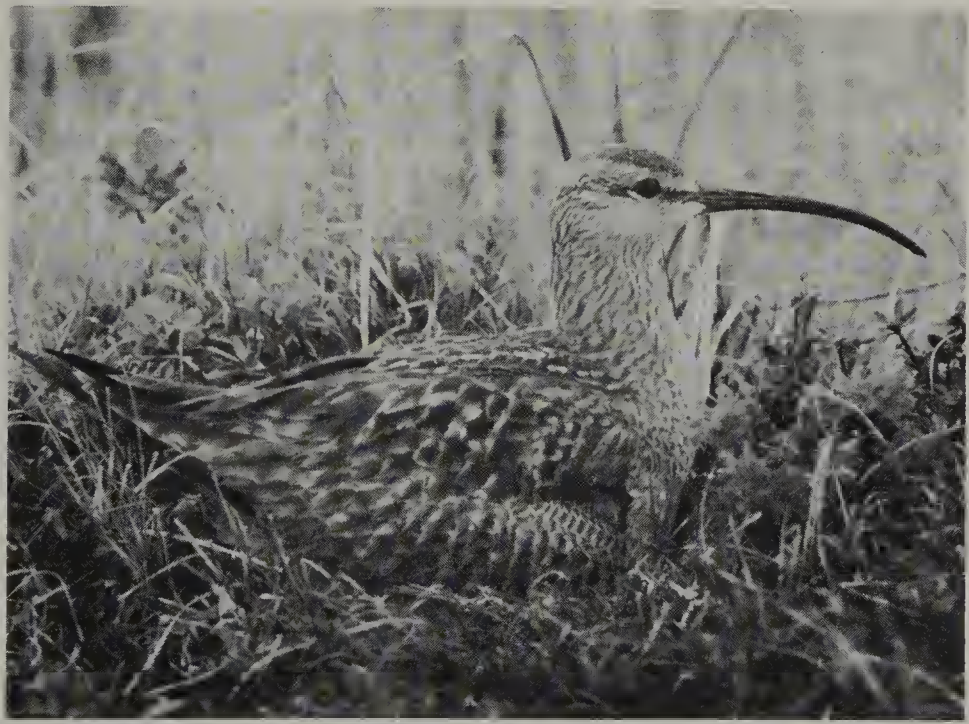
In comparing alpine tundra in Wyoming and arctic tundra in Alaska, Bliss (1956) found several differences with respect to importance of various kinds of plants. Thus heaths, lichens, and mosses are important in the arctic, but rare in Wyoming tundra. On the other hand, the alpine tundra of Mt. Washington, New Hampshire, shows closer floristic relations with arctic tundra than with western alpine tundras (Bliss, 1963). Thus on Mt. Washington as in the arctic, mosses, lichens, and heaths are prominent. Plants having shallowly rooted rhizomes are important in the arctic, whereas in Wyoming alpine tundra plant roots penetrate the soil to greater depths (Bliss, 1956).

Herbaceous vascular plants common in the tundra (Fig. 5-9) include grasses, sedges, saxifrages, rushes, legumes, sedums, and fireweeds. Important shrubs include willows, alder, cranberry, birches, heather, and leatherleaf. In general, the number of species increases as one goes from north to south, undoubtedly due to the less rigorous climate of the low arctic compared to the high arctic.

The animals of the tundra include species present and active the year round as well as forms which migrate or hibernate. In one way or another, these organisms have found a way to survive the long, cold winters.

Larger animals of the arctic tundra include the herbivorous musk ox and barren ground caribou, the carnivorous tundra wolf and polar bear, and the omnivorous barren ground grizzly bear. Smaller forms include the arctic fox, arctic hare, collared lemming, muskeg meadow mouse, willow ptarmigan, snowy owl, and northern horned lark. These are all permanent year-round active species except for the caribou, which migrates south for the winter, and the grizzly bear, which dens up for the winter. The arctic ground squirrel hibernates on hillsides where permafrost does not reach. Lemmings are probably the most abundant mammals and are active throughout the year, burrowing under the snow or in the mat of vegetation. Many waterfowl come to the arctic during the summer to reproduce, then migrate south for the winter (Fig. 5-10). Reptiles are practically nonexistent, as are amphibians, although Shelford and Twomey (1941) noted the presence of a gartersnake and a frog near Churchill, Manitoba.

Invertebrate species are less numerous than at lower latitudes, but are definitely not uncommon. At Churchill, Shelford and Twomey (1941) found 74 genera of Diptera, with only a few genera of Coleoptera, Lepidoptera, Hymenoptera, and spiders. McClure (1943) collected over 400 species of invertebrates near Churchill in a two-month study. Certain species may be exceedingly abundant, such as blackflies and mosquitoes. Thus McClure (1943) on one occasion collected 2,000 specimens of blackflies in 50 successive sweeps of a net. Invertebrates may overwinter as larvae or pupae, although



Ralph S. Palmer

Fig. 5-10 A representative breeding bird of the tundra, the Hudsonian curlew, *Numenius phaeopus hudsonicus,* incubating.

some species, such as beetles, may pass the winter as adults.

The numerous ponds are inhabited by various insects, especially beetles, as well as a few species of snails, leeches, cladocerans, flatworms, and possibly a frog. Fishes are few; they are primarily migratory in nature and mostly occur in streams rather than in the numerous but shallow ponds.

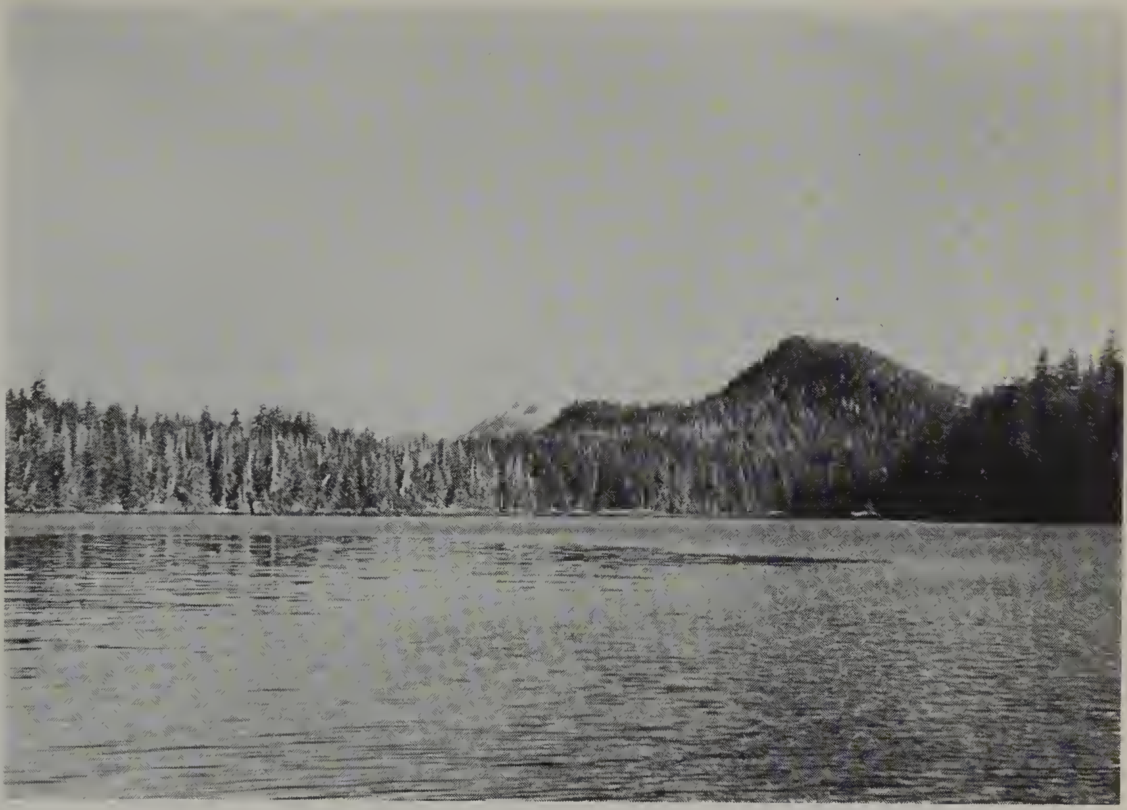
Despite the more than 10,000 papers that have been written on arctic biology, there is probably less known of this biome than any other. Until recently, there were relatively few detailed studies of arctic communities. Even today, there is a need for extensive and comprehensive studies of this biome. Because of its inaccessibility and rigorous climate most research has been made during summer months only and at only a few places.

Very little is known of either communities or individual species of the arctic. Little is known of the various facets of the life cycles of plant species that adapt themselves to the rigorous climate, such as their propagation and dispersal mechanisms (Polunin, 1955). Genetic studies are needed to determine whether dwarf forms are short because of the climate or because of genetic constitution. Interactions of plants and animals, such as the effect of grazing of lemmings on lichens, require attention (Britton, 1957). The origin and other aspects of arctic soils are imperfectly known.

Finally, as mentioned earlier, the arctic itself is undergoing change, and this causes complexity of communities which makes an understanding of their dynamics difficult. For example, Banfield (1958) has shown that the range of the barren ground grizzly bear has been steadily increasing since 1900. This spread is probably thc result of the earlier spread of the range of an important food species. This species, the arctic ground squirrel (*Citellus undulatus*), is probably itself invading territory that has been colonized by plants following the retreat of the last glacier. There is evidence (Raup, 1941) that the tundra is extending northward in some areas but southward in others.

Taiga

The *taiga* biome is characterized by the dominance of coniferous trees in its climax communities and is sometimes known as the boreal forest because of its northern location (Fig. 5-11). It forms a continuous belt across the continent from Newfoundland in the east to Alaska in the west. In the



Allan G. Heath

Fig. 5-11 The taiga near Craig, Prince of Wales Island, at the southern tip of Alaska (latitude about 56° N). Note the slender form of the trees and their crowded condition, which permits very little herbaceous growth underneath.

east it extends south to the Great Lakes and at higher elevations of the Appalachians to the Carolinas. West of Minnesota, the southern boundary goes up to Saskatchewan, and then continues west to the Pacific, dipping southward along the Rockies to New Mexico, down the Cascade Range and the Sierra Nevada to Mexico, and down the Coast Ranges as far south as central California. Along the coast from Cook Inlet, Alaska, going south, rainfall is much higher than in other parts of the biome, so that this region is sometimes referred to as a coniferous rain forest.

In general, the taiga may be characterized as a biome having dense forests of narrow-leaved evergreen trees. Temperatures are cold in the winter, the growing season relatively short, and precipitation fairly low. The topography is mostly post-glacial, with many lakes and bogs and poorly drained, thin, acid, mineral soils (Fig. 5-12).

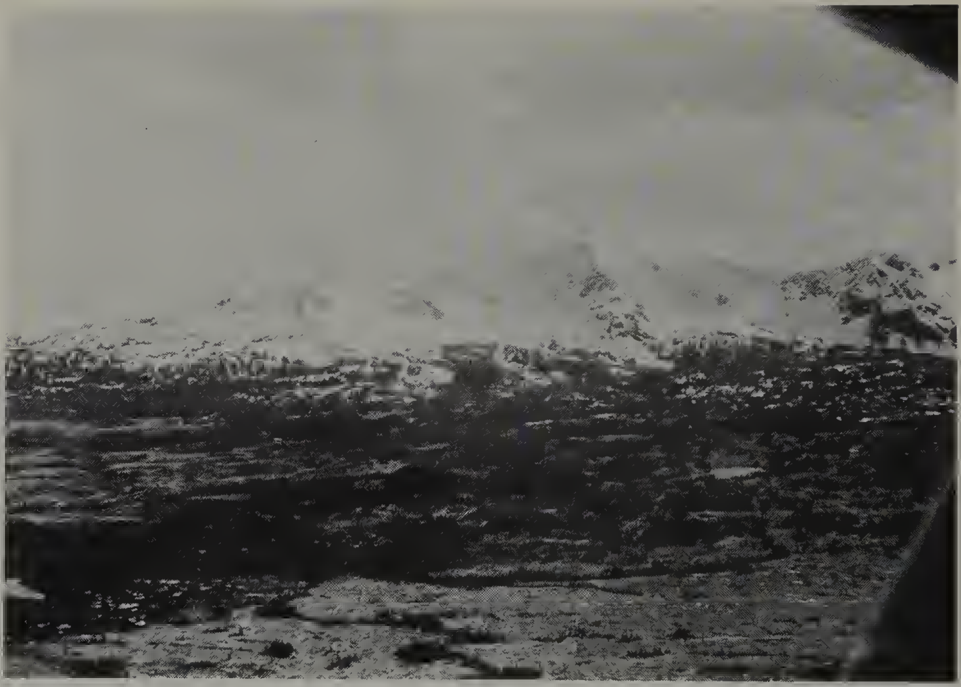


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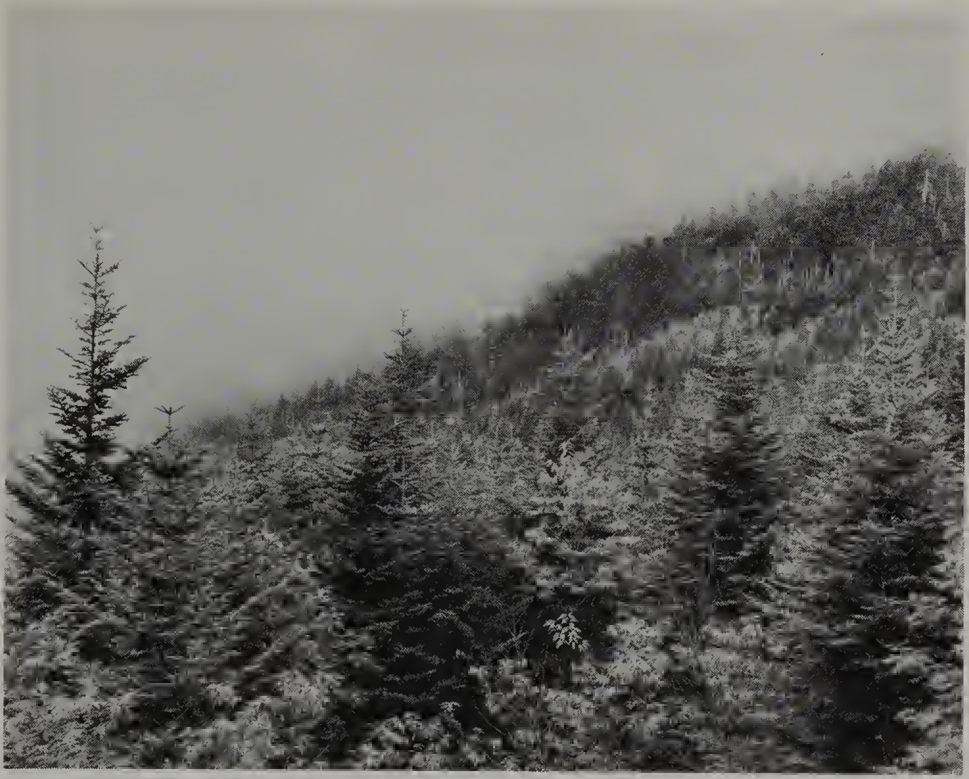
Fig. 5-12 The taiga near its northern limits, intermingled with tundra to form an ecotone, near Seward, Alaska, latitude 60° N.

No one physical factor seems to be of dominating importance throughout the biome. Winter temperatures average well below the freezing point, and permafrost is found in the colder, more northern and continental parts of the biome (Sjörs, 1961). Summer temperatures may climb as high as 100° Fahrenheit, but the average is probably closer to 60° to 70° Fahrenheit. In the Pacific rain forest area, the climate is much milder, with winter temperatures averaging near freezing and summer temperatures averaging about 70° Fahrenheit. The lack of extreme temperatures and the high humidity and rainfall of the coastal region are due to oceanic influences.

Precipitation averages from 15 to 40 inches a year throughout most of the biome, with nearly half of it occurring during the summer (Fig. 5-13). In the rain forest area it may range from 50 to 150 inches, most of it falling from October to May. This area is humid and often foggy. In places, as much as 50 inches of precipitation a year may occur as fog condensed on vegetation (Oberlander, 1956). The waxy nature of the evergreen leaves of the conifer is also highly efficient at preventing water loss through the leaf epidermis.



William E. Werner, Jr.

Fig. 5-13 The taiga in the Appalachians, near its southern limits, on Clingman's Dome, Great Smoky Mountain National Park, at about 6,600-feet elevation. Note the clouds, often present in summer, from which these mountains get their name.

Snow may be of importance in certain regions. Depth of snow accumulation may be great in some areas. For example, in northern Michigan as much as 115 to 130 inches may fall in one winter. This may be one of the important factors in determining community types in this area (Maycock, 1961). Pruitt (1958) noted that snow is involved in a regular and significant disturbance of the coniferous forest in Alaska. This is possible because relatively windless periods allow heavy accumulations of snow on the trees and cause them to snap. Other species may then invade the disturbed area.

The growing season varies from approximately 60 to 150 days depending on location throughout the continental taiga, and to nearly 300 days on the Pacific coast. However, the "frost-proof" evergreen leaf is well adapted to making good use of short warm spells and sunny weather outside the frost-free period of the growing season, so that productivity is high.

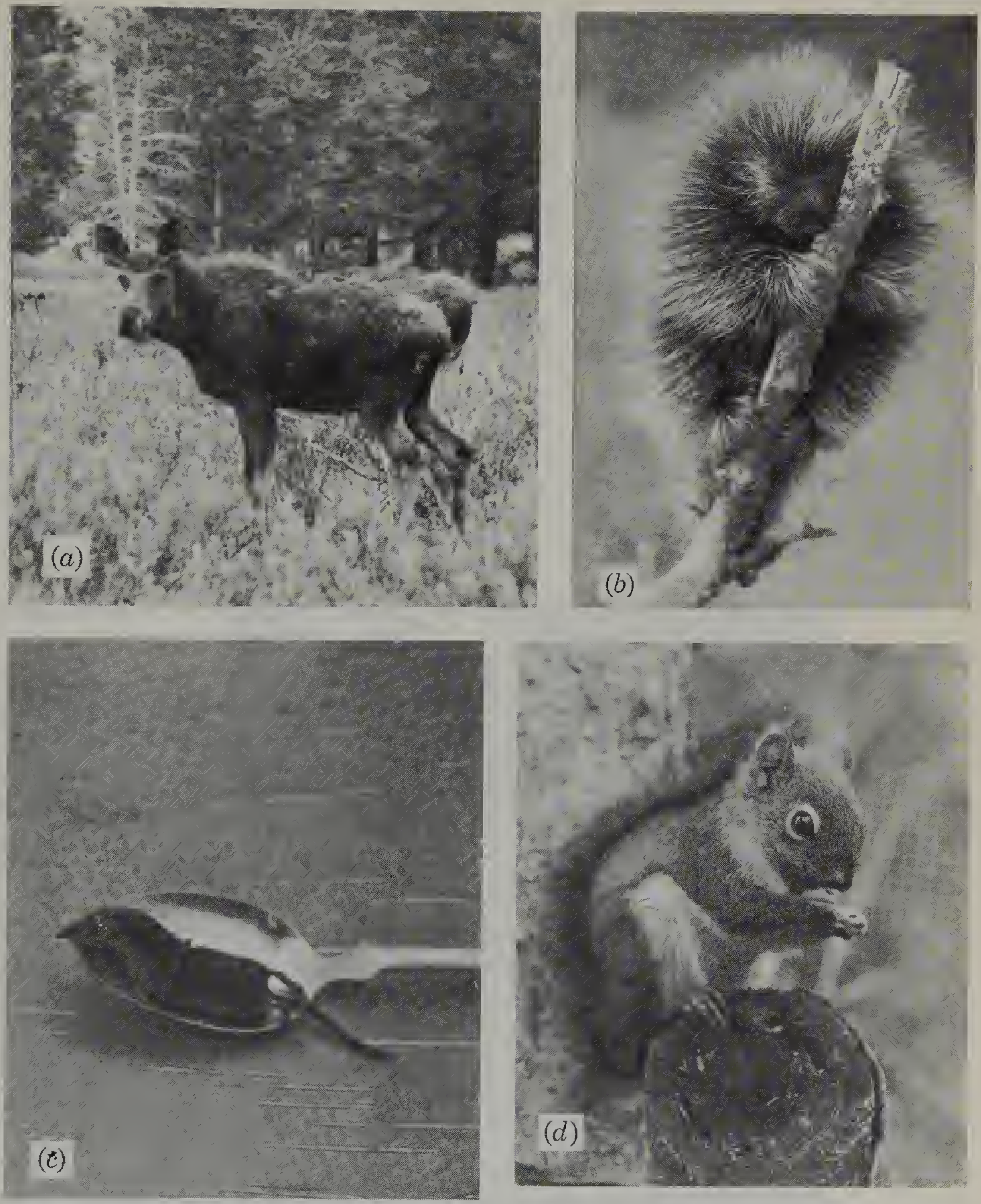
The climax forests of the taiga are dominated by spruces and firs. Buell and Niering (1957), in comparing the coniferous forests of Minnesota, New England, and North Carolina, concluded that despite the fact that only a few species were common to these three areas, ecological equivalents are present in each, and the forests are therefore very similar (Fig. 5-13). Thus, in the northeast, white spruce is dominant, but is replaced in New England by red spruce. From Lake Superior west, black spruce is a dominant across western Canada to the northern limits of the taiga. Similarly, balsam fir of the northeast is replaced by Frazer fir in the Appalachian mountains of North Carolina. Tamarack, while present in the East, becomes a dominant in the West, especially northward.

In the mountains of the West, similar ecological equivalents are found, but replacements become more extensive with varying conditions imposed by latitude, elevation, and proximity to the Pacific Ocean. In the Rockies, subalpine forests are dominated by Englemann spruce and to a lesser extent by alpine fir. Below this zone, Douglas fir dominates, with some grand fir and white spruce in the north and white fir and blue spruce to the south. In the Sierras, red fir, mountain hemlock, and white fir dominate in subalpine situations, and various species of pine take over to the south. In the montane forests of the Cascades, white fir, incense cedar, Douglas fir, and several pines (sugar, Jeffrey, and ponderosa) become important. Along the Pacific coast in Alaska, Sitka spruce and white spruce dominate. To the south, white spruce is replaced by western and mountain hemlock. Near Puget Sound, western arborvitae and grand fir dominate. Redwood becomes dominant south to central California; Douglas fir remains common but not as a dominant. In the coastal mountains, alpine fir, mountain hemlock, and other firs are dominant at higher elevations, Douglas fir and western arborvitae at lower altitudes.

The conifers grow so close together that relatively few shrubs and herbs are to be found. Viburnums, heaths, small maples, and yew are some of the shrubs of the biome. Club mosses, and a few spring-flowering plants are characteristic. Mosses, such as sphagnum, may blanket the ground.

The seral communities occupy more area in the biome than do the climax communities (Shelford and Olsen, 1935). Thus one finds communities dominated by pines, alders, willows, birches, aspens, and poplars throughout the biome.

The taiga has been called the moose-spruce biome because

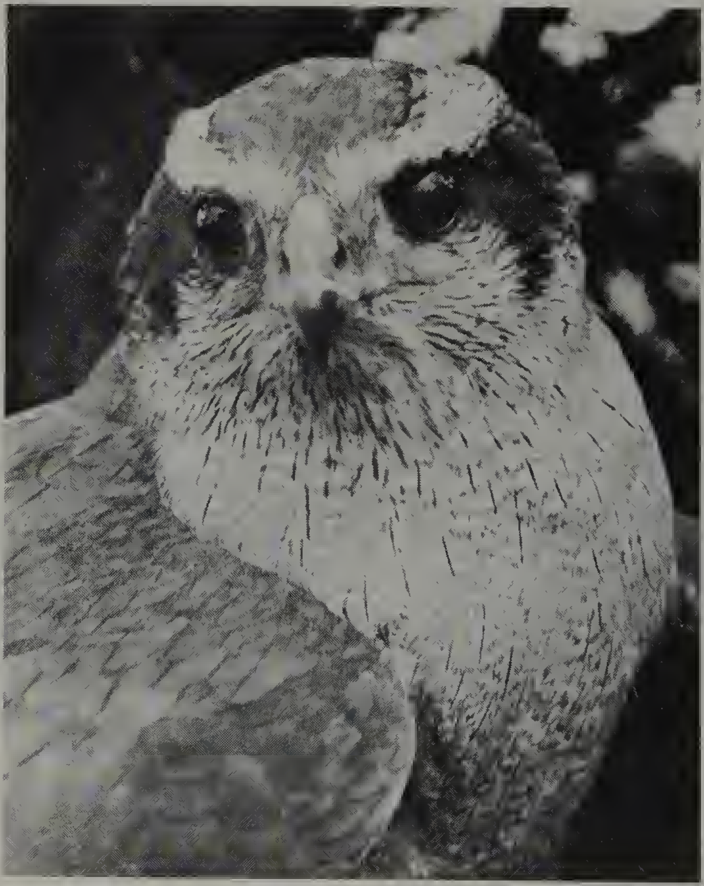


Ralph S. Palmer

Fig. 5-14 Representative mammals of the taiga:
(*a*) Moose, *Alces americana.*
(*b*) Porcupine, *Erethizon dorsatum.*
(*c*) Pigmy shrew, *Microsorex hoyi.*
(*d*) Red squirrel, *Tamiasciurus hudsonicus.*

of the prevalence of these species within it. Certainly the moose is one of the largest animals of the taiga (Fig. 5-14). Equally characteristic are the black bear, marten, fisher, porcupine, phenacomys, red-backed vole, red squirrel, northern flying squirrel, and spruce grouse, which live mostly in the climax forests, although they may range over seral communities as well. Other important vertebrates are the caribou, gray wolf, lynx, wolverine, red fox, varying hare, Canada jay, yellow warbler, northern flicker, hairy woodpecker, Hudsonian chickadee, goshawk (Fig. 5-15), and horned owl.

Certain kinds of invertebrates are common, especially Diptera, including blackflies, no-see-ums, and mosquitoes. Of special significance are the bark beetles, larch sawfly, and spruce budworms, which on occasion may devastate forests. The cold winters require most invertebrates to hibernate and limit the number of species of amphibians and reptiles. Birds



E. G. Tabor

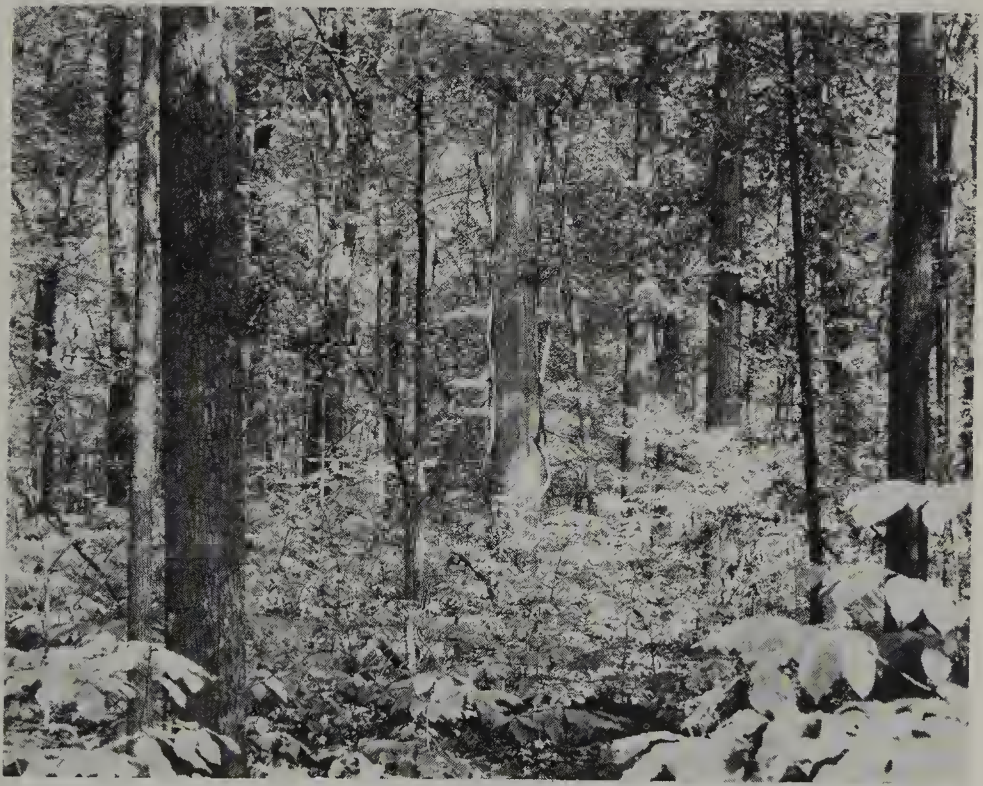
Fig. 5-15 The goshawk, *Accipiter gentilis*, a breeding bird and an important predator of the taiga.

are common in this biome as summer residents, but most species tend to nest in the numerous seral communities rather than in the conifers. The bills of a few birds such as the crossbills are adapted to extract seeds from cones.

Several fine studies have been made of coniferous forest communities in critical areas. More work, however, is needed in correlating physical conditions with local communities, as in the work of Daubenmire (1956) and Whittaker (1960). Also, more intensive study of the role of animal components of communities would be helpful. Finally, transition areas between the taiga and adjacent biomes need further study.

Deciduous Forest

The deciduous forest biome (Fig. 5-16) occurs south of the taiga in the eastern half of the United States, extending west to just beyond the Mississippi River into Missouri, Arkansas, and parts of Iowa, Kansas, and Texas. Along stream valleys, however, it extends still farther west. It includes most of the Appa-



Soil Conservation Service, U.S.D.A.

Fig. 5-16 The deciduous forest biome; a virgin forest in Kentucky.

lachians except those regions high enough to be a part of the taiga or tundra. The southern part of Florida (from Tampa and Orlando south) is sometimes excluded from the biome because of its subtropical climate (see p. 148).

As the name of this biome implies, the dominant trees of its climax communities are usually deciduous, although evergreens may be dominants in climax and seral communities. The forests are usually stratified with a small tree layer under the canopy of taller trees and a layer of shrubs under the small trees. The forest floor usually has a limited number of spring-, summer-, and fall-flowering plants and ferns. The climate is temperate, with moderately cold winters and warm summers. Precipitation is relatively high compared to evaporation and falls more or less evenly throughout the year.

The annual temperatures of the biome vary about 30° Fahrenheit from north to south. Toward the north of the biome, normal annual temperatures average about 45° Fahrenheit, whereas in the southern extremes the average annual temperature climbs to about 75° Fahrenheit. Winter temperatures vary from an average of about 25° Fahrenheit in the north to 65° Fahrenheit in the south. Winter low extremes may vary from −20° Fahrenheit in the north to 30° Fahrenheit in the south, summer high extremes from 118° Fahrenheit in the north to 120° Fahrenheit in the south.

Normal annual precipitation within the biome varies from about 25 inches in the northwest and 35 inches in the southwest to about 50 inches in the northeast and 60 inches in the southeast. Precipitation is in excess of evaporation, this excess increasing from less than an inch in the west to about 20 inches in the east. From 50 to 70 per cent of the precipitation falls during the crop-growing season with the remaining precipitation spread out over the remaining months (Visher, 1954).

The growing season varies considerably from north to south. Along parts of the Great Lakes it may be only 120 days, while the majority of the northeastern region enjoys a longer period—up to 200 days. In the southern area it varies from 200 to 300 days.

The preponderance and presence of various species of dominant trees of the deciduous forest biome varies from north to south and east to west, reflecting differences in climate, topography, soils, and recent geography (only the northern part of the biome was glaciated). The literature on the complex vegetation of this area has been summarized by Braun (1950).

Along the Great Lakes, maple and beech are common, in combination with hemlock in the east and basswood toward the Midwest. White pine may also be common. Along the northern part of the Atlantic coast, white, red, and chestnut oaks predominate. The chestnut was once a dominant in this and other parts of the biome, and its destruction by a blight has caused a readjustment which is still incomplete. Toward the south, along the Piedmont and Coastal Plain to Virginia, other species such as the tulip tree become more common.

Pine barrens occur only sporadically along the coast from New England south to Virginia. On the Piedmont Plateau and continuing across the states bordering the Gulf of Mexico, however, pines and broad-leaved evergreens become abundant. This part of the deciduous forest biome is sometimes known as the southern evergreen forest. Disturbance by fire and other causes have allowed pines (especially pitch, loblolly, yellow, longleaf, and slash) to become numerous. Live oaks and other evergreen oaks, magnolia, and holly are other common trees of this area, which increase the evergreen effect. Spanish moss frequently festoons the trees giving these communities an additional distinctiveness.

All these species do not occur together, but certain species are characteristically associated with each other. For example, longleaf pine and scrubby oaks often dominate on dry hills, while longleaf, loblolly, and slash pine may occur together on poorly drained flat lands. On moist slopes, white beech may be common with tulip tree. In the northern part of this evergreen forest, loblolly pine and oaks may be associated. Along the southern part of the coastal states, slash pine may be abundant in pure stands or with other pines and evergreen oaks. On the Atlantic and Gulf Coastal Plain, longleaf pine, magnolia, and live oak frequently occur as dominants. On river bluffs in the southernmost coastal area from Georgia to Mississippi, beech and evergreen magnolias may dominate. In swamps, cypress is common along with swamp tupelo and pond pines.

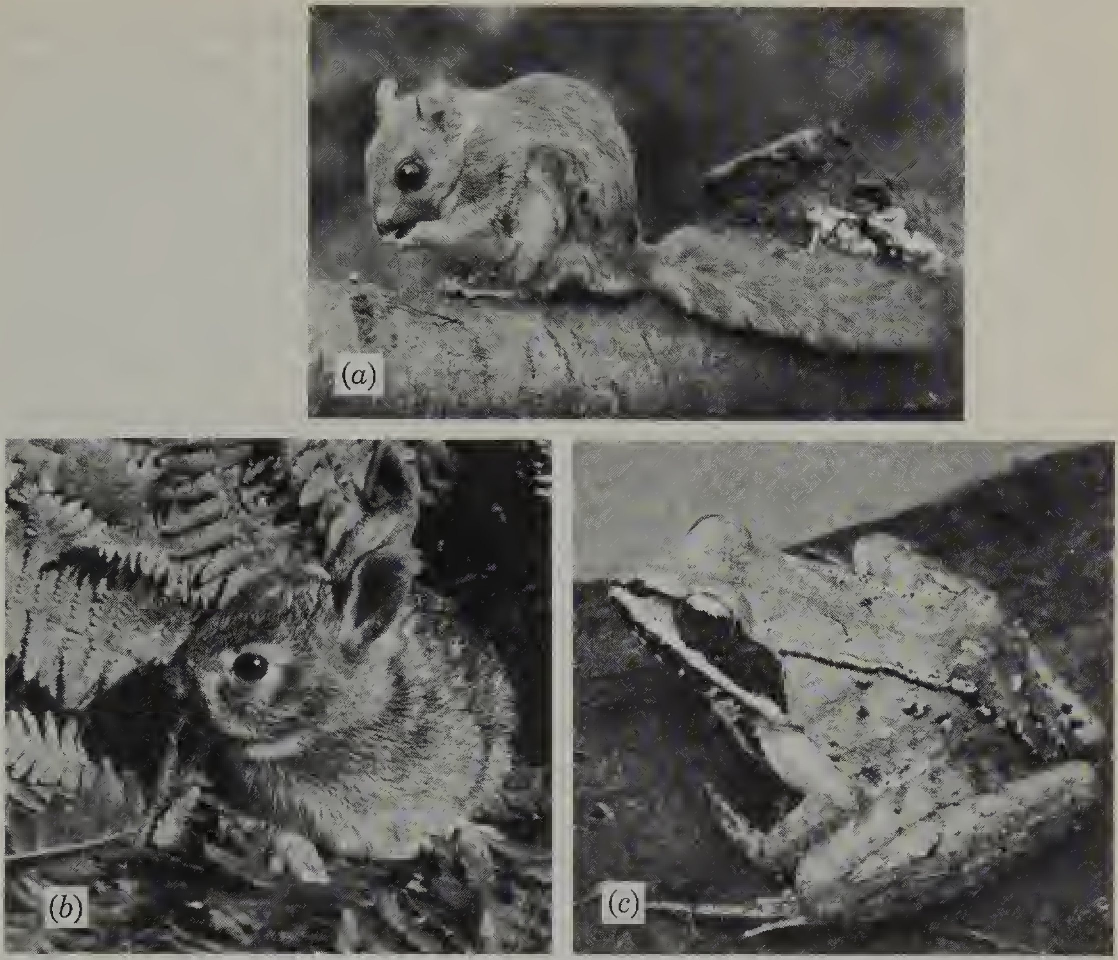
In the Alleghenies and Appalachians a wide variety of tree species may be found, including hemlock, sugar maple, buckeyes, basswoods, beech, tulip tree, and red and white oaks. Hickories, birches, ashes, cherries, black gum and pines are among the common trees to be found in non-climax communities. The topography of the mountains provides variations in soil, moisture, and exposure to sun, rainfall, and temperature, which affect the species composition of the communities. The vegetational analysis of an area of the Smoky Mountains by Whittaker (1956) is an example of a fine study correlating certain environmental conditions with species composition in a floristically critical area.

West of the Appalachians the precipitation-evaporation ratio becomes critical for trees, so that trees which require less moisture predominate, especially oaks and hickories. There are numerous species of oaks and hickories, but only a few of them are wide-ranging, the rest occurring commonly only in certain geographical areas. In Ohio and Indiana beech, maple, and tulip trees are found as dominants; they become less common as the western limits of the biome are approached. In northern Illinois and Wisconsin, there is evidence that Indian burnings maintained the oak-hickory forests, and that present protection from fire will allow development of a maple-basswood forest (Braun, 1950). To the south and west, hickories and oaks become more important; in the Ozarks they may be the only dominants.

The fauna of the deciduous forest biome is richer than that of the other two biomes thus far considered. This is true of both invertebrates and vertebrates. Among mammals, Virginia deer, raccoon, opossum, red and gray foxes, striped skunk, eastern gray and fox squirrels, white-footed and deer mice, eastern mole, and short-tailed shrew are typical (Fig. 5-17). Some animals such as bear, mountain lion, bobcat, and timber wolf were once found throughout the biome but have been nearly eliminated.

Amphibians and reptiles are abundant, becoming more numerous in species toward the west and south. Typical species include snapping turtles, stinkpot turtles, box turtles, painted turtles, fence lizards, five-lined skinks, red-bellied snakes, brown snakes, water snakes, eastern garter snakes, eastern ribbon snakes, ringneck snakes, milk snakes, copperheads, timber rattlers, newts, spotted salamanders, American toads, Fowler's toads, spring peepers, cricket frogs, leopard frogs, green frogs, and wood frogs (Fig. 5-17*c*).

Insects are numerous and varied, as are other invertebrates. In one study of a 60-acre tract in Illinois, approximately 500 species of invertebrates were collected (Shelford, 1951). Total populations varied with the weather, season,



Ralph S. Palmer

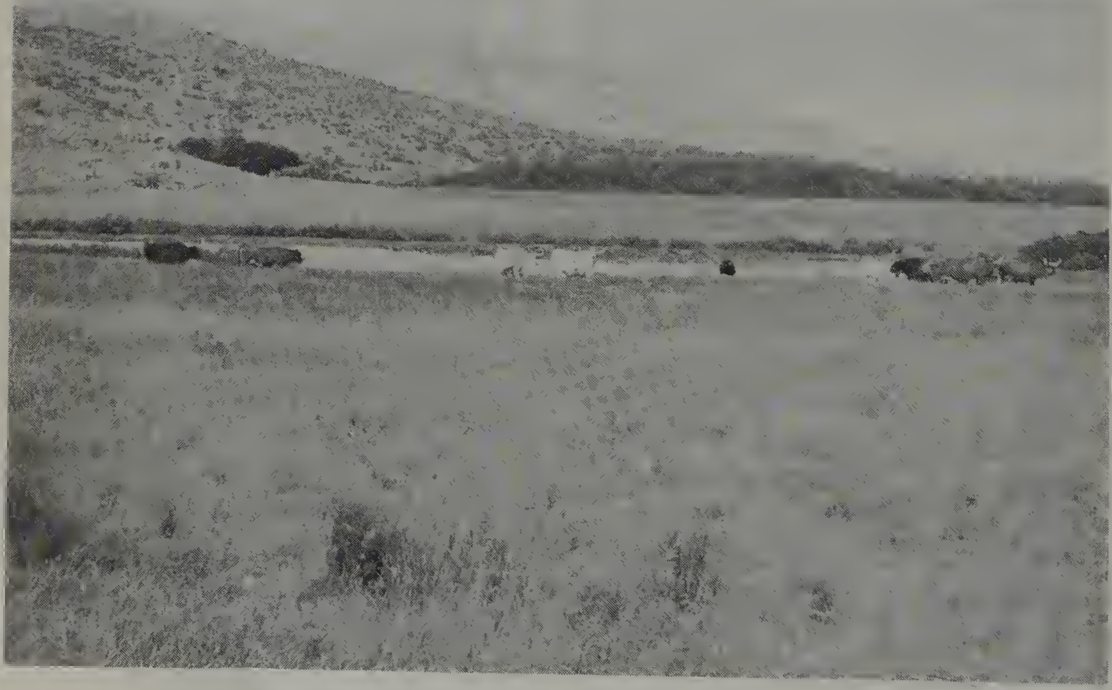
Fig. 5-17 Some representative animals of the deciduous forest biome:
(*a*) Flying squirrel, *Glaucomys volans.*
(*b*) Eastern cottontail, *Sylvilagus floridanus.*
(*c*) Wood frog, *Rana sylvatica.*

and year from 280 to 1,700 per square meter. The organic matter on the forest floor, as well as the first few inches of topsoil, is often rich in invertebrates. Rotting logs provide another type of habitat favored by a variety of small forest animals. Other species inhabit herbs and shrubs, while still others, such as borers, prefer trees.

This biome has been studied intensively, yet there are still many problems which require solution. There are indications that the climate is changing slightly, allowing some species to extend their ranges northward. Before this biome was colonized by the white man, the Indian had disturbed communities by burning, sometimes accidentally, sometimes to provide open areas for hunting. Natural disturbances, such as hurricanes, insect damage, and diseases (Dutch elm disease and chestnut blight, for example), have affected communities in varying degrees. The agricultural and other activities of the present human population have destroyed much of the forest. In a large area of the northeast, where lumbering and fires have made serious inroads on the forest, the trees reproduce primarily by sprouting, thereby affecting community composition. Paradoxically, some areas are now better protected from fire than they were in pre-colonial times, and these forests are just now beginning to show the effects of this protection.

Grassland

The grassland biome (Fig. 5-18) extends from the western boundaries of the deciduous forest biome to the foothills of the Rocky Mountains in the west and from southern Alberta and Saskatchewan in Canada south to Texas. Isolated patches in Ohio and extensive parts of central Indiana and Illinois are within the biome as well as a crescent-shaped region in Alabama and Louisiana. The northern boundary passes at an angle from northern Illinois across the southern parts of Min-



Allen H. Benton

Fig. 5-18 A short-grass prairie in the Wichita Mountains Wildlife Refuge, Oklahoma. The cattle are old-style longhorns.

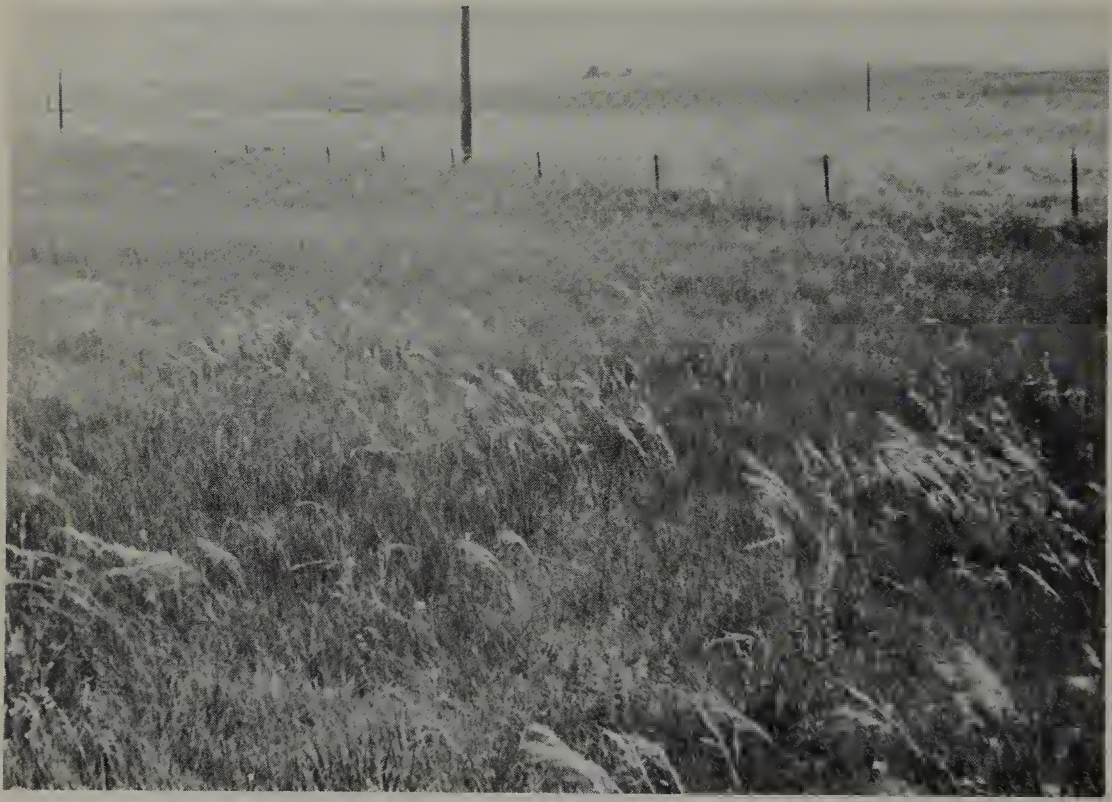
nesota, Wisconsin, Saskatchewan, and Alberta. In addition, an isolated area of about 25,000 square miles called the Palouse region in eastern Washington and Oregon and western Idaho, and the grasslands of the Great Valley of California, are part of this biome.

The essential feature of the grasslands is the growth form of the dominant plants—grasses. The grasses toward the east are tall (4 to 10 feet), while those of the western limits are short (less than 2 feet). The central part of the biome is characterized by a mixture of tall and short grasses. The climate is one of extremes and of variations in rainfall over an extended period of time. Prior to the arrival of the white man, large herds of herbivores roamed the grasslands, and fire often swept the vast seas of grass. Today, much of the grassland is under cultivation or is heavily grazed by cattle. Protection from fire is also causing vegetational changes in some areas, especially toward the east.

Of all the facets of the climate, probably the most important to organisms in this biome is the rainfall-evaporation ratio. Rainfall increases toward the east and south as evaporation decreases. In general, then, the biome becomes drier in its western reaches, and this is reflected in the height of the grasses. Annual rainfall averages about 10 inches in the west to nearly 40 inches in the east and south. Toward the northeast, as in Minnesota, it may be as little as 20 to 26 inches (Tester and Marshall, 1961) and only 14 to 16 inches in Saskatchewan (Coupland, 1961). Rainfall occurs mostly in the spring and early summer except in the California grasslands, where it falls primarily during the winter. However, rainfall is irregular and droughts may occur at any time.

The temperatures of the grassland are lower toward the north, especially in the winter, when they may reach −50° Fahrenheit (Looman, 1963). In Saskatchewan, the average temperature during the growing season is about 54° to 58° Fahrenheit (Coupland, 1961). Late-summer dry spells with accompanying high temperatures are characteristic of the grasslands.

Winds are often strong and help to increase aridity. According to Weaver and Albertson (1956), wind velocities are higher on the Great Plains than anywhere except at the seashore. (An exception to this might be mountaintops.) In Saskatchewan, Looman (1963) noted that chinooks (warm southwest winds) may raise the temperature from below zero



William E. Werner, Jr.

Fig. 5-19 A short-grass plain in Colorado.

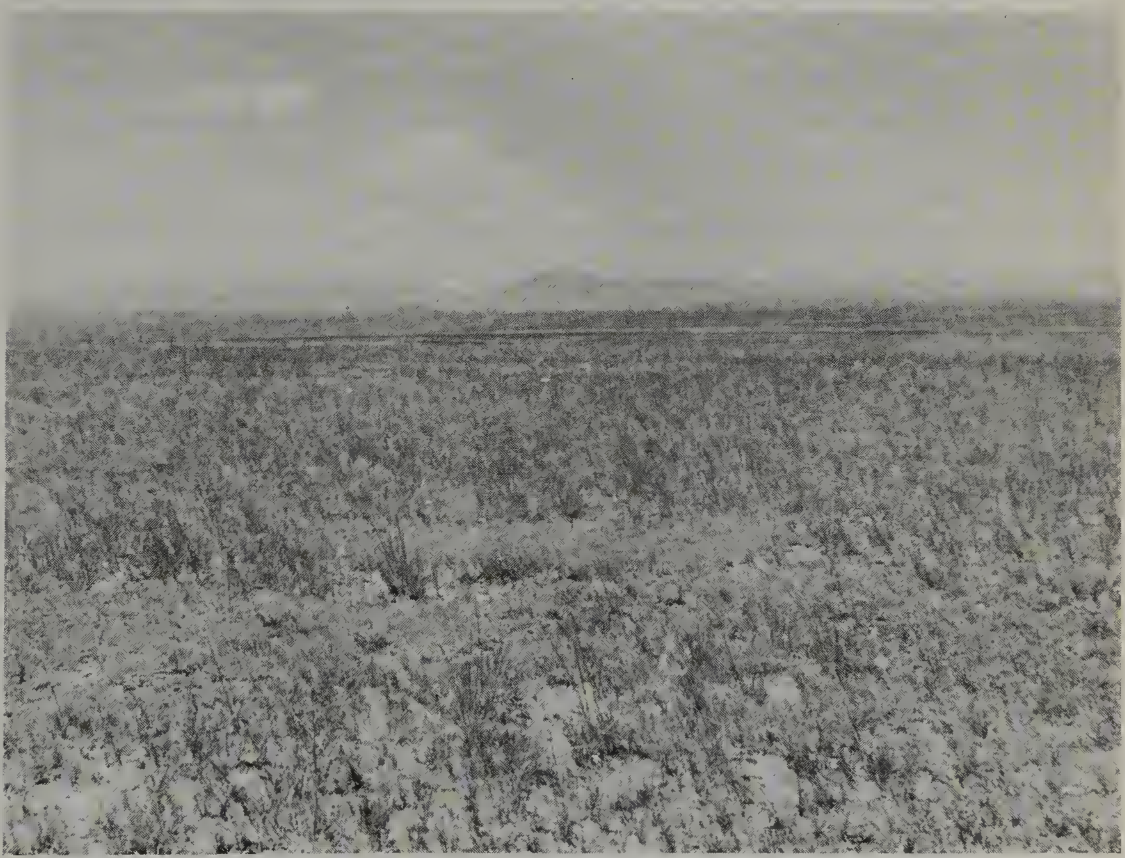
to above freezing in a few hours. Such temperature changes are not uncommon in this treeless, level expanse, where fronts may move rapidly up from the Gulf of Mexico, down from Canada, or across the Rockies.

The growing season ranges from 110 to 120 days in the north to 365 days in the south, where frosts are almost unknown.

Soils vary, but include black, dark brown, and brown earths. Low rainfall and high evaporation rates, coupled with absorption by plants, result in the concentration of lime at shallow depths (8 to 18 inches) in the west to 6 feet or deeper in the east. In the west, the deeper soil is not moist, and the water table is below the reach of the plant roots (Weaver and Albertson, 1956). The soils are relatively unleached, poorly drained, and fertile. Their textures and structures are favorable to plant growth, especially grasses, which can withstand the low winter rainfall, unreliable snow cover, and occasional summer drought (Weaver, 1954).

The grasslands in general are flat but not featureless. The eastern prairies are dissected by tributaries of the Mississippi, while in the Great Plains erosion has produced sand hills, loess plains, hilly buttes, mesas, canyons, badlands, and stream terraces. In the north, there are other features resulting from recent glaciation.

The vegetation is dominated by grasses, although forbs (other non-woody plants) may form a large part of the plant species. In the east, the grasses form a sod, with roots penetrating to about 11 feet (Weaver, 1954). Some of the species, such as big bluestem, buffalo grass, and wheat grass, have numerous rhizomes. Other species are bunch grasses and grow in clumps, such as little bluestem, June grass, and needle grass. Toward the west, the sod becomes lighter, and in the extreme western part of the biome, plants are separated by bare soil, and roots do not penetrate as deep (Fig. 5-20). Many plants of this biome have a life span of 10 to 20 years, some longer (Weaver, 1954). Where annual grasses domi-



William E. Werner, Jr.

Fig. 5-20 A short-grass prairie in Wyoming.

nate, one can suspect that recent disturbance to the community has occurred.

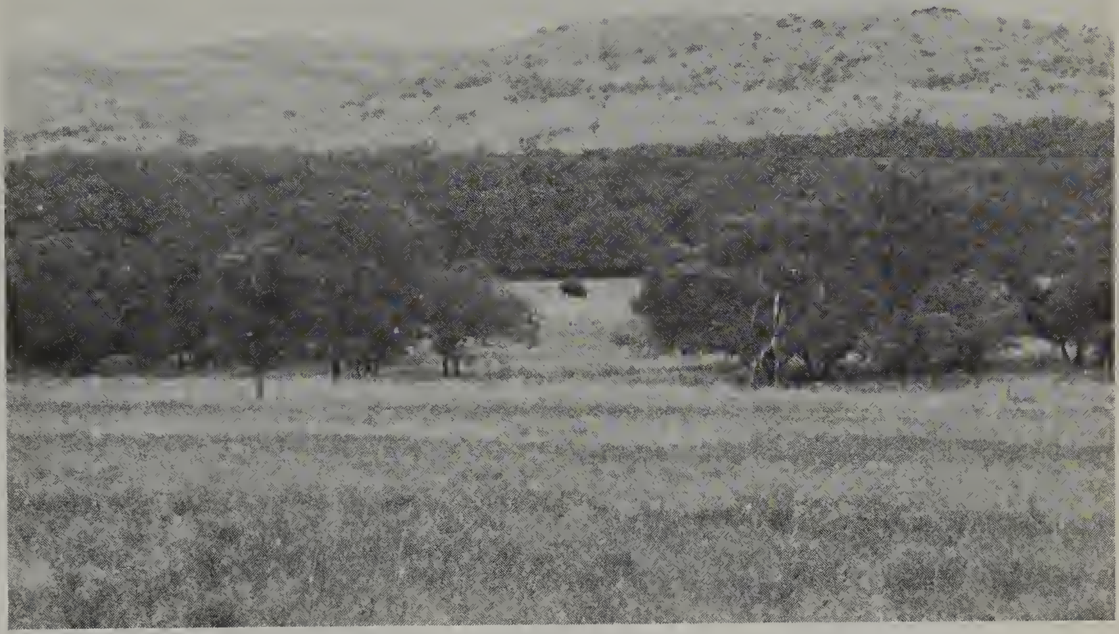
The grassland biome has sometimes been divided into the tall-grass prairie, mixed-grass prairie, and short-grass plains. The tall-grass prairie in Ohio, Indiana, and Illinois has considerably more rainfall than other parts of the biome, and in the last few centuries before the coming of the white man may have been maintained as grassland only by the effects of fire, grazing and trampling by buffalo.

The tall-grass prairie extends from the deciduous forest to the eastern parts of Saskatchewan, North and South Dakota, Kansas, Nebraska, and Texas. Big bluestem, switch grass, and slough grass are species often found as dominants in the lowlands, with Indian grass and Kentucky bluegrass (an introduction from Europe) occasionally abundant. On the uplands, little bluestem, side oats grama, June grass, needle grass, and prairie dropseed are commonly the dominants. These grasses may form communities in various combinations with one another and with numerous forbs. The upland species tend to be shorter and more often form bunches. Those species of grasses which dominate on the uplands in the eastern part of the biome are often found on slopes farther west; in the western part of the biome they may occupy wet, lowland habitats (Carpenter, 1940).

Within the prairie there are other communities, occurring on sandhills, river flood plains, and land disturbed by man. These communities may be dominated by trees or may be seral communities. In some areas, such as that described by Tester and Marshall (1961) in Minnesota, the prairie has been maintained by fires. With recent fire control and drainage, the prairie in such places is being invaded by aspen and willow.

Transition from forest to tall-grass prairie may be abrupt or gradual. In some areas there may be savannas of oaks and grasslands (Fig. 5-21). An even more gradual transition in Oklahoma is described by Penfound (1962), where blackjack oak and post oak become gradually dwarfed from 50-foot trees in the east to 20-foot trees in the west. Since the crowns of the trees remained close together, this does not seem to be quite a savanna, but rather a pigmy forest.

West of the tall-grass prairie, the biome is dominated by short and tall grasses, including needle and thread, green needle grass, sand dropseed, western wheat grass, June grass, blue grama, side oats grama, three-awned grasses, and buffalo



Allen H. Benton

Fig. 5-21 A post-oak–short-grass prairie ecotone in western Oklahoma. A bison is grazing in the center of the picture.

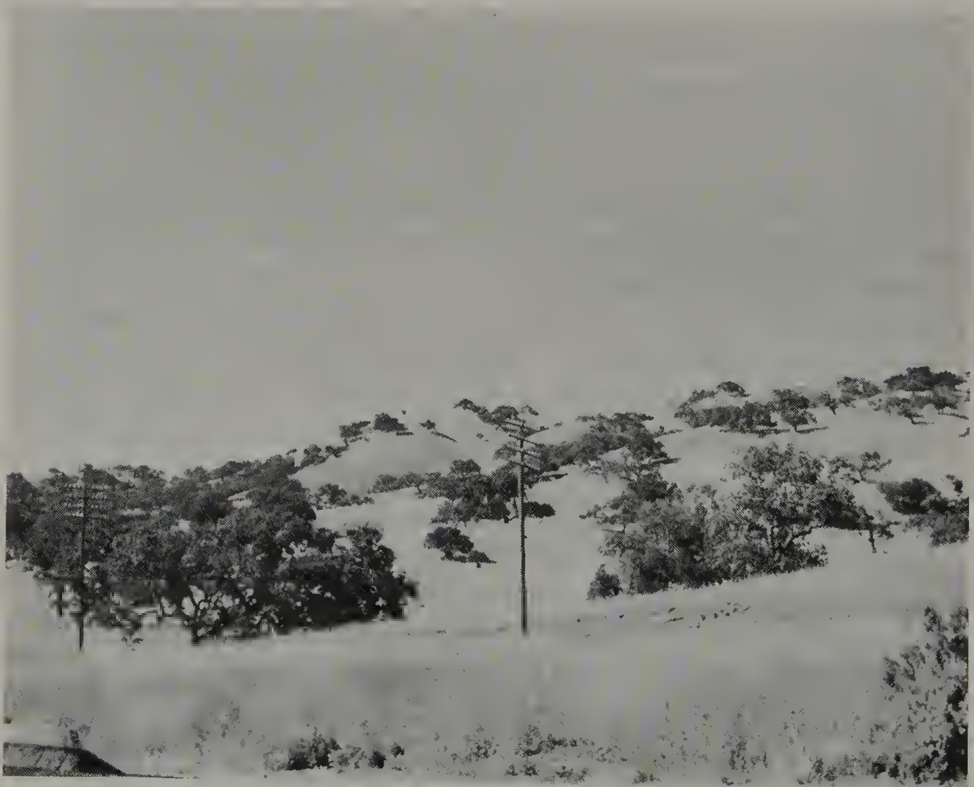
grass. Other species may also be dominant locally. Blue grama, three-awned grasses, and buffalo grass are short grasses and can withstand grazing better than the taller grasses. The central grassland community (also called the Great Plains) changes toward the western limits of the grassland biome into a short-grass community. Thus the Great Plains is often divided into a mixed-grass prairie and short-grass plains. Weaver and Albertson (1956) contend, however, that the short-grass community is a result of overgrazing, during which taller grasses are killed, leaving only the short grasses. Drought may have a similar effect. Hurd (1961) found that overgrazing changed the grassland community, with protection against overgrazing allowing development of wheat grasses, brome grass, fescue, and bluegrass. Coupland (1961) also found that grazing in Saskatchewan led to the development of a community more typical of a xeric situation. In southwest Texas and southern Arizona, extreme overgrazing led to development of communities with mesquite, creosote bush, and cactus.

The stable prairie communities of Saskatchewan and

Alberta are dominated by needle grass and wheat grass, and in the extreme northwest, by fescue. In the Palouse region, the dominants are primarily wheat grass (in dry areas) and fescue (in moist areas). The grasslands of central California (Fig. 5-22) were probably originally a mixed prairie dominated by bunch grasses, especially needle grass (Burcham, 1957).

Before colonization of the grasslands, large herds of buffalo and smaller ones of antelope migrated from one area to another. Because they were not restricted in their movements, they did not destroy their food supply, although certainly their trampling, fertilizing, and wallowing had their effects on the community.

Most of the herbivores of the American grasslands are small. They include ground squirrels, prairie dogs, jack rabbits, gophers, and many species of mice, including the prairie meadow mouse and the prairie deer mouse. Predaceous mammals of the grassland include the badger, spotted skunk, coyote, and kit fox. Relatively few species of birds breed here,



William E. Werner, Jr.

Fig. 5-22 Savanna-type community in California, near Buellton, Santa Barbara County. Grass dominated between widely spaced live oak trees.

possibly a reflection of the lack of trees. Many nest on the ground, and several have flight songs. Prominent among the bird species of the grassland are the meadowlark, bobolink, longspurs, horned lark, upland plover, rodent-eating hawks, and prairie chickens.

Reptiles and amphibians find the grasslands a suitable habitat. The largest numbers of species of these animals in the United States are found in Texas, with most prairie states also having large numbers. Typical grassland species include speckled king snakes, rough green snakes, Plains garter snakes, bull snakes, eastern yellow-bellied racers, western hog-nosed snakes, prairie rattlesnakes, ornate box turtles, snapping turtles, smooth soft-shell turtles, map turtles, six-lined race runners, Great Plains skinks, Plains spadefoot toads, Great Plains toads, Blanchard's cricket frogs, chorus frogs, small-mouthed salamanders, and tiger salamanders.

Insects find the grasslands a suitable habitat too. Especially abundant are grasshoppers, crickets, and leafhoppers. Spiders are also numerous. Carpenter (1940) found that in eastern Kansas, populations of insects and spiders were greater in seral communities than in climax communities and that 97 per cent of the insects hibernating in the grassland are in the ground litter and crowns of grasses. These hibernators are therefore obliged to become active early in the spring to avoid being drowned.

The grassland biome is at first glance a simple one. This is a deception, however, as many of the studies that have been made of the area indicate. Among other things, the condition of the climax communities before the coming of the white man is not known in most cases. Also, the influence of Indian fires is uncertain, although we are beginning to see the effects of fire control in some areas. Finally, the effect of the periodic droughts and overgrazing on community composition, especially in the western part of the biome, is a continuing problem of great economic importance.

Desert

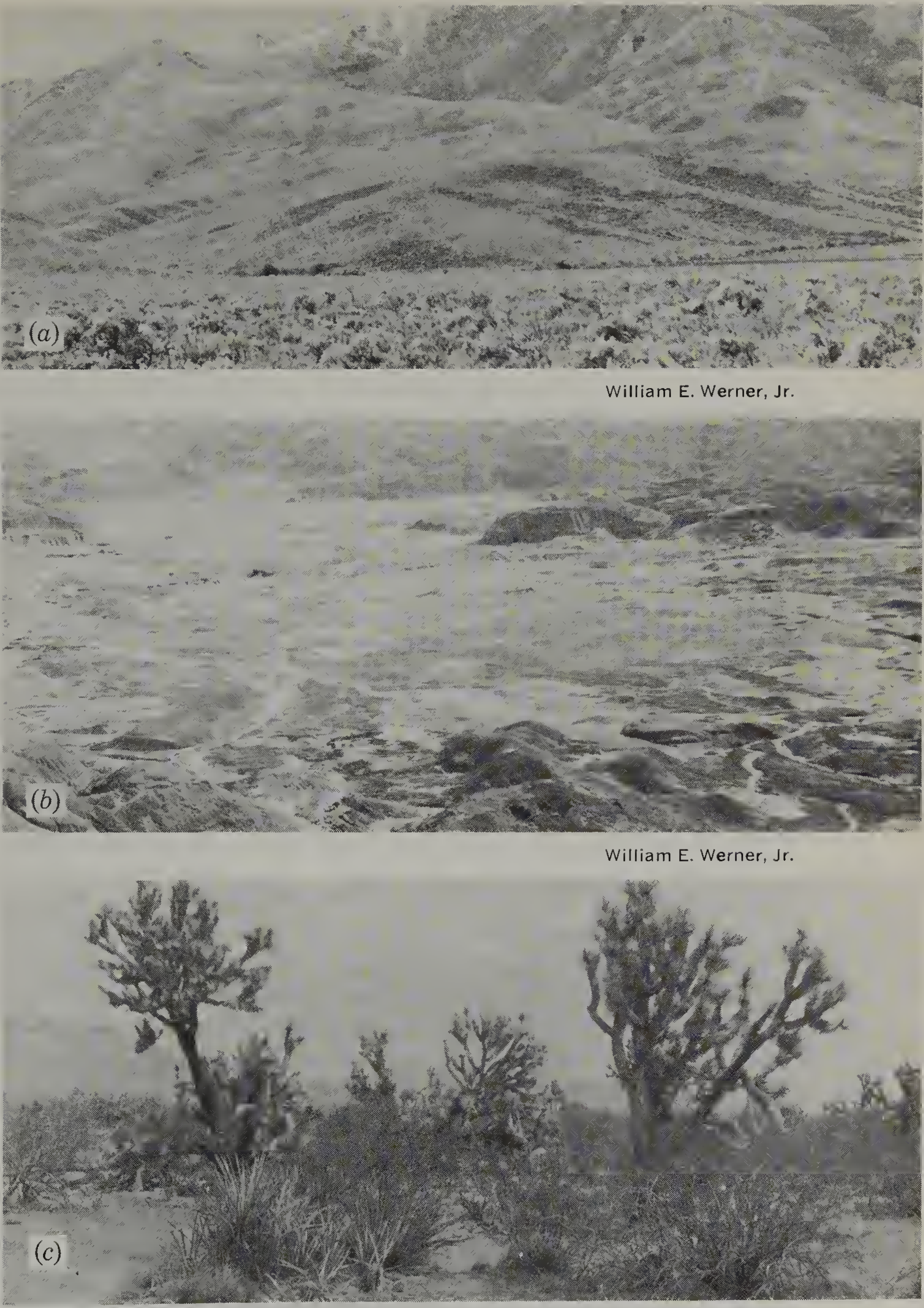
The desert biome of North America occurs in the western part of the United States between the Rocky Mountains and the Sierra Nevada into Mexico. It includes four deserts: the Great Basin of southwest Oregon, southern Idaho, Nevada, the southwest corner of Wyoming, and most of Utah; the Mohave in the lower tip of Nevada, an adjacent portion of California, and the northwest corner of Arizona; the Sonoran in southeast California, southwest Arizona, most of Baja California, and the adjacent Mexican mainland; and the Chihuahuan of central New Mexico and the Mexican plateau (Fig. 5-23).

The desert is characterized by harsh environmental conditions. Rainfall varies from 2 to 16 inches a year, and daytime summer temperatures are the highest of any biome. Vegetation is relatively sparse and dominated by shrubs, succulents, and dwarf trees. Animals are either adapted physiologically to survive in the hot, dry environment or able to avoid the extreme conditions by burrowing or by being inactive during the heat of the day.

Rainfall is probably the most important single physical factor of the desert. In general, it is greatest in the north or at higher elevations and least in the south or at lower elevations. Throughout the desert, rainfall is uncertain and very unevenly distributed, so that some areas may receive no rain, while other regions may experience heavy showers. This is especially true in the summer when local torrential cloudbursts may produce a flood which does the vegetation little good, since it quickly runs off the surface into a streambed. The hot summer sun and low relative humidity cause quick evaporation of the little rain that may have soaked into the soil.

Extreme temperatures are the second of the important physical factors of the desert. In the northern Great Basin Desert, maximum daytime temperatures may reach 115° Fahrenheit in midsummer, but in most places 105° Fahrenheit is a more likely maximum. In the Imperial Valley of the Sonoran Desert, however, maximum temperatures of 134° Fahrenheit have been recorded. Soil temperatures go even higher during the day. Winter minimum temperatures may fall to −30° Fahrenheit in the north and to well below freezing in the southern deserts. However, some areas of these southern deserts may never experience frost. Southern desert forms cannot withstand heavy frost and may suffer severe damage by an occasional cold spell (Fautin, 1946). The daily temperature fluctuations may be great—as much as 20° Fahrenheit in winter and 55° Fahrenheit in summer. In part this is due to an absence of cloud cover, allowing rapid reradiation of heat back into the atmosphere at night.

Humidity is low in the desert as one would expect. It is lowest at midday, highest at night, with the greatest fluctuation occurring in summer when the daily temperature range



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William E. Werner, Jr.

Donald H. Miller

Fig. 5-23 The desert biome:
(*a*) A "cool" desert in northern Nevada.
(*b*) A "hot" desert, the Painted Desert in Arizona.
(*c*) A "hot" desert in Arizona, dominated by Joshua trees, *Yucca brevifolia.*

is also the greatest. Of great significance is the amount of water that is evaporated in the desert. Thus at various areas of the Mohave, evaporation of 85, 87, 90, and 116 inches of water a year have been recorded, far beyond the average 5 inches or so of precipitation for the area (Jaeger, 1938).

Part of the great evaporation is of course due to high temperatures, but much of it is caused by the high daily winds. In the northern deserts, winds average about 11 miles per hour but may reach maximums above 40 miles per hour (Fautin, 1946). The winds occur daily, often declining at sunset.

Soils vary in color and texture from light to dark and fine to gravelly. The volcanic rocks and soil are dark while other soils are lighter. Where salts are abundant, as in alkaline soils, the surface may be light to white. If drainage is poor, mud flats or dry lakes (playas) may form, and if salts are present wet surfaces (salinas) result. Parts of the desert are hilly and mountainous, but flat areas between hills are common. These plains may be at varying altitudes from below sea level to several thousand feet.

The growing season varies from north to south. In the northern deserts it may be as short as 120 days, while in some southern deserts, such as the Salton Sink of the Sonoran Desert, it is 365 days. However, lack of adequate rainfall in warm seasons tends to make comparisons of the length of the growing season of the desert with other biomes meaningless.

Despite the rigors of the desert, many species of plants representing a large number of families are to be found. Jaeger (1938) states that there are at least 700 species in the California deserts alone. Wright (1959) lists as common plants over 250 species belonging to 56 families and 169 genera in west-central and southwestern Arizona.

One might expect to find that plant reproduction in the desert would be difficult because of the short rainy season and that, as a result, many plants would be perennials. This in fact seems to be the case. Fautin (1946) found that in the northern deserts 81 per cent of the plants were perennials, and that all native dominant grasses were perennials. The floral season is brief (6 to 12 weeks), its length depending on the rainfall of a particular season. Flowers often do not result in seeds because droughts may occur before the seeds can mature.

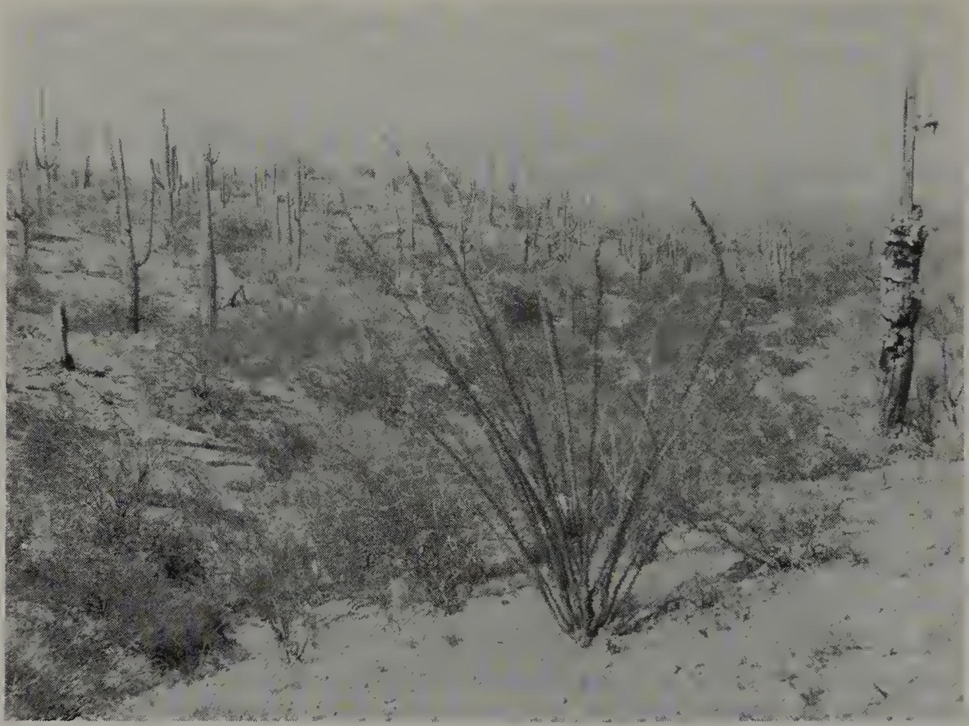
Lack of water is undoubtedly the greatest difficulty for plants to overcome. Many perennial species have adaptations that are thought to help them in this respect, including reduction of leaf surface, shedding of leaves in hot seasons, waxy epidermis, extreme hairiness of leaves, and increased osmolar concentrations of cell substances. Despite these features, many desert plants still transpire large amounts of water, and wilt. However, they are able to recover from wilting, and this may be one of their greatest adaptations for desert life. Among the annual plants, there are no special drought-resistant vegetative features. Instead, their seeds are so adapted that they will germinate only when there has been a soaking rain (½ to 2 inches) in the late fall (Went, 1955).

The northern part of the biome is sometimes called the "cold desert." This is the desert of the Great Basin, which lies mostly at an elevation of 4,000 feet or more. Rainfall is more or less well distributed throughout the year. In areas where rainfall is highest (averaging about 15 inches a year) sagebrush communities are found. These occur especially at bases of mountain ranges or in valleys with deep soil relatively free of mineral salts.

If the water table is no more than 15 to 25 feet below the surface but salt is present, the community will probably be dominated by greasewood, with salt blite as a common associate (Fautin, 1946). Where rainfall is lower (about 8 inches a year) or mineral salts are present, the dominant plant is often shadscale, a shrub with both a deep tap root and an extensive surface root system. Greasewood may also be common in such situations, along with winterfat and bud sage (Fautin, 1946).

The southern deserts (Mohave, Sonoran and Chihuahuan) are called the "hot deserts." In general, precipitation is lower and occurs irregularly throughout the year, while both summer and winter temperatures are warmer. The rainfall over most of the Mohave is 5 inches or less and is highest around its margins. Throughout this desert, there are only a few dominant species in the communities. At the bases of the numerous mountains the dominants (Joshua tree, sagebrush, creosote bush, and *Tetradymia*) are taller. Farther from the mountains they are all smaller, the Joshua trees become scarce, and burroweed tends to replace *Tetradymia* as an important shrub (Shreve, 1942).

In the Sonoran Desert, creosote bush and burroweed are the dominants, with cholla cactus as an important associate. On rocky slopes saguaro, ocotillo, and palo verde may dominate



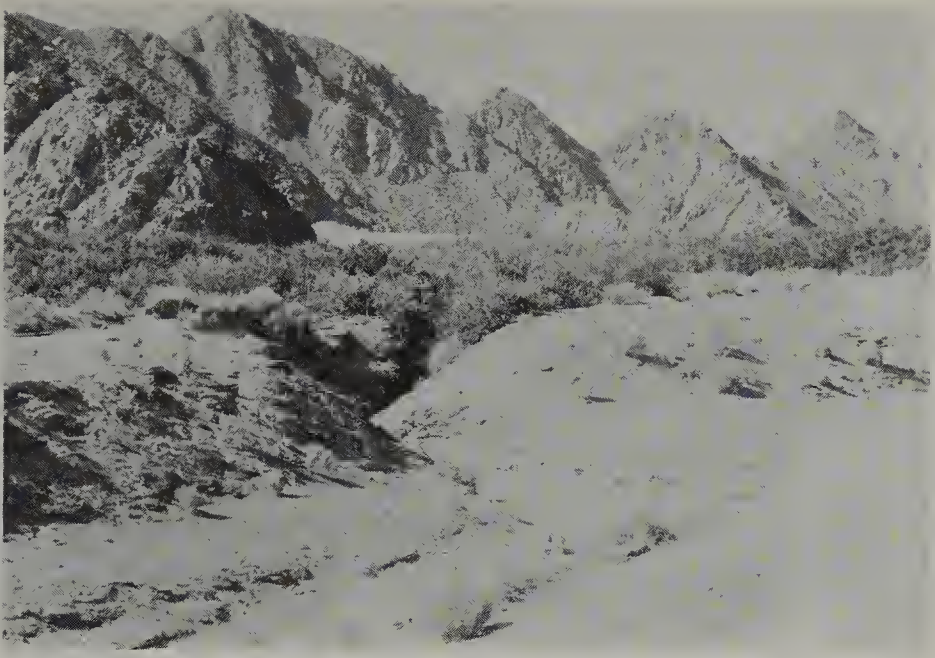
Donald H. Miller

Fig. 5-24 The Sonoran Desert near Tucson, Arizona, showing two of the dominant plants of this community, saguaro (background) and ocotillo (foreground).

(Fig 5-24). Along water courses mesquite is common (Fig. 5-25). The most distinguishing vegetative feature of the Sonoran Desert is the many species of cacti (Dice, 1939). Most of this desert lies below 2,000 feet, and is level or slightly tilted. Along the Gulf of California rainfall is only 2 to 4 inches a year, but inland and at higher elevations it may climb to 14 inches.

In the Chihuahuan Desert, most of the rain falls in summer and amounts to 3 to 16 inches a year. Trees are found only along streams or on rocky slopes. Shrubs and semishrubs are dominant, while various cacti and large semisucculents may be conspicuous.

Of the desert animals, mammals often assume the most important role in the community. Many of them have special adaptations for surviving in a hot climate where drinking water is scarce or absent. Fautin (1946) noted that 68 per cent of the mammals of the northern desert were nocturnal and that nocturnal animals were most abundant in open com-

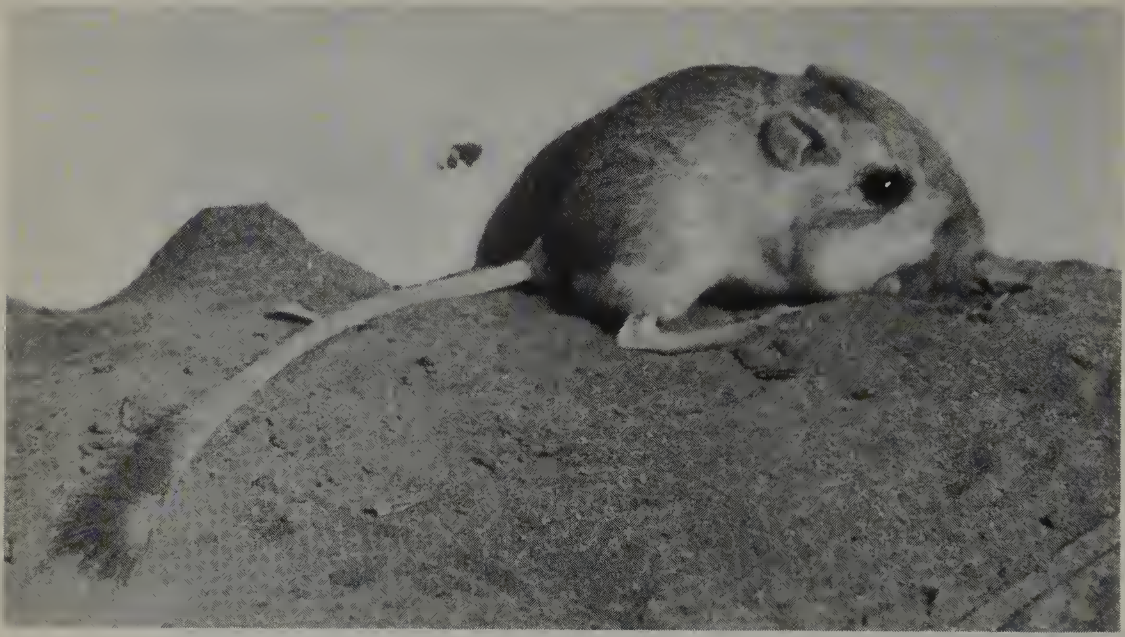


William E. Werner, Jr.

Fig. 5-25 A dry wash in the Sonoran Desert, 10 miles south of Palm Springs, California. Mesquite is common along the banks of the "stream."

munities, such as those dominated by shadscale. Nocturnal activity reduces evaporation, since at night temperatures are cooler and relative humidities higher. Another way animals may escape the high temperatures of the desert is to burrow. Bodenheimer (1957) calculated that 72 per cent of desert mammal species burrow in contrast to 47 per cent in shortgrass prairies and 6 per cent in forests. Many mammals of the desert are light in color. The significance of this fact is disputed (Buxton, 1923; Dice, 1939) since there are many dark soils in the desert as well as light ones. Light color may be a response to low humidity or to a combination of factors.

Many mammals live on seeds and grasses and obtain their water from metabolic processes. Very few perspire, and most pass little urine (Jaeger, 1938). Rodents, especially mice, are the most numerous mammals of the desert. Fautin (1946) considers the kangaroo rat the most important rodent of the shadscale community, and badger, kit fox, coyote, and antelope as the major mammals of the northern desert in general (Fig. 5-26). In the southern deserts, the same major species occur, and many of the other species are the same. Several species are endemic to this area, including round-



Ralph S. Palmer

Fig. 5-26 The kangaroo rat, *Dipodomys merriami*, a typical desert mammal.

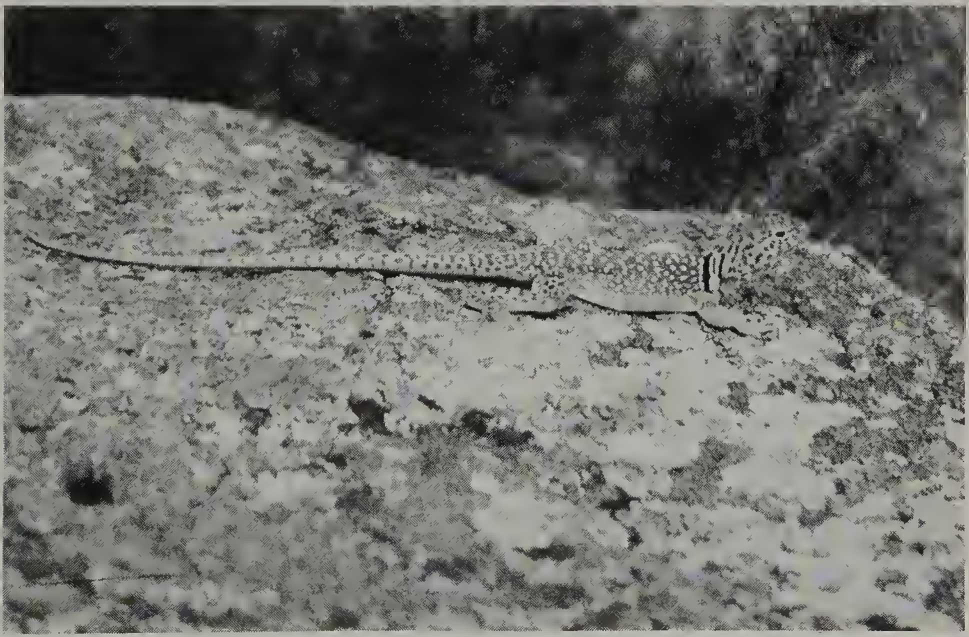
tailed ground squirrels, Mohave ground squirrels, Sonoran and Mohave kangaroo rats, and several mice, like the cactus mouse and pocket mouse (Dice, 1939).

Birds also show adaptations for desert life. Most have pallid coloration, which probably helps to reflect light and acts as camouflage. Most species nest on the ground on the shady side of plants. Flight is rapid, and nearly all fly low to avoid enemies and the intense wind (Fautin, 1946). Birds do not have special adaptations to overcome the water problem, however, and must obtain their water from the food they eat or find springs or rivers. At least some species, like the cactus wren and thrashers, nest early and cut down on the number of eggs, or forego both nesting and egg laying during drought years (Jaeger, 1938). Important birds of northern deserts include Swainson's hawks, marsh hawks, prairie hawks, and western burrowing owls (Fautin, 1946). Jaeger (1938) lists Say's phoebes, ravens, road runners, horned larks, Gambel quails, white-rumped shrikes, verdins, plumbeous gnatcatchers, and LeConte and Crissal thrashers as endemics of the southern deserts.

Reptiles have very few physiological adaptations to the desert. Because of their limited tolerance to both high and low temperatures, their seasonal and daily activity periods are short (Fautin, 1946). Their glandless, keratinized integument is well adapted to prevent water loss, and their urine and feces are passed with a minimum of water. Water is obtained from the bodies of their prey, from vegetation, or from their metabolic processes.

Lizards are the most commonly encountered reptiles, and snakes are relatively rare. Fautin (1946) noted that 40 per cent of all snakes seen during his study were rattlesnakes, which are inactive only during the hottest part of the day. Some lizards are herbivores, some are carnivores, and others are omnivores. Common reptilian species in northern deserts include collared lizards, horned toads, Utas, striped racers, gopher snakes, and rattlesnakes (Fig. 5-27). Important southern desert forms include chuckwallas, Gila monsters, several Utas, horned toads, and desert tortoises.

Amphibians are restricted to moist regions and are relatively rare in desert communities. The Colorado river toad, red-spotted toad, Pacific tree toad, and sand-colored tree toad are among the species present. Extensive irrigation systems being built in parts of the desert are allowing amphibians to penetrate the area, in many cases bringing formerly isolated species together.



Allen H. Benton

Fig. 5-27 The collared lizard, *Crotaphytus collaris,* a common inhabitant of deserts and semideserts.

Invertebrates of the desert include primarily insects, spiders, and other arthropods. Some insects estivate; some eat food of high water content; but most are able to withstand the drought of the desert by physiological adaptations such as waterproof bodies, excretion of solid uric acid, and production of metabolic water (Jaeger, 1938). Many species are nocturnal, while some, like grasshoppers, are diurnal but spend the hottest part of the day in the shade.

Fautin (1946) noted that in one northern desert, invertebrates were distributed in layers—shrub and ground. Where shrubs were more closely spaced and were more or less evergreens and in the sagebrush and greasewood communities, insects remained abundant further into the summer than in the shadscale community, where shrubs were widely spaced and defoliate with the approach of hot weather.

Tropical Biomes

The part of the world between the Tropic of Cancer and the Tropic of Capricorn is called the tropics. In North America, this includes the southern part of Mexico, Central America, and the islands of the Caribbean. Tropical conditions, however, may extend into temperate latitudes because of the influence of the ocean, and temperate conditions may penetrate the tropics along the mountain ranges. There is, therefore, no distinct biological or climatic or geographical demarcation of the tropics, and there is a lack of general agreement on boundaries, largely depending on one's definition of "tropical."

Within the tropics are several biomes, including evergreen broadleaf forest, deciduous forest, savanna or grassland, thorn forest, and desert. Although the tropical deciduous forest, grassland, and desert biomes are distinct from their temperate counterparts, the broadleaf evergreen (tropical rain) forest is the most unusual and will receive the bulk of the discussion of these biomes here.

A common misconception of the tropics is that they are not as disturbed by man as are the temperate biomes. However, man has lived in the tropics a long time, so that much of the area is not in its "primitive" state. As Gill (1931) pointed out, pre-Columbian Central American Indians used wood extensively and set fire to forests for various reasons. A large part of this region might have been forest, for example, but is instead grassland because of the activities of the Indians.

Tropical Rain Forest

The broadleaf evergreen forest biome is sometimes called the rain forest and, more popularly, the jungle. It occurs along the eastern coast of Mexico below the Tropic of Cancer, on the Yucatan Peninsula, in British Honduras, and in the eastern part of Guatemala, Honduras, Nicaragua, and Panama. Parts of Cuba, Haiti, the Dominican Republic, Jamaica, and Trinidad also have this biome, although the forests have largely been destroyed or seriously altered by man's activities on these islands.

The climax communities of the tropical rain forest biome are dominated by tall evergreen broadleaf trees. The biome occurs in regions of the tropics where rainfall is plentiful and well distributed throughout the year and where the temperatures are high and relatively uniform.

Rainfall is probably the most important physical factor limiting the extent of the tropical rain forest toward the temperate zones. Probably as little as 60 inches of rain per year might allow development of a rain forest if there were no dry spell (less than 2 inches of rain in one month), but usually 80 inches or more a year is required to produce a rain forest. With high rainfall, dry periods of up to five months may still allow presence of a rain forest, although it may not be as luxurious (Richards, 1952).

The frequent and abundant rains, along with the tall, dense forests, promote an atmosphere of high humidity. At midday, when air temperatures are highest, the relative humidity may fall as low as 55 per cent, but at other times of the day it is much higher and generally reaches near saturation at night. The forest, however, slows down the wind, so that evaporation on the forest floor may be only half that occurring near the canopy (Allee, 1926*a*). Still, where flecks of sunlight reach the forest floor, evaporation at noon may be very great.

Temperatures in the tropics are high but not as high as in some temperate deserts. In general, the mean average temperature ranges from 68° to 82° Fahrenheit. However, the variation from the warmest to coolest seasons averages only 41° Fahrenheit or less, and in the rain forest the coolest month will have a mean temperature of only 77° Fahrenheit. Near the equator, day length may vary from 11 to 13 hours throughout the year, while at the temperate-tropics boundary the variation is from a 10-hour day to a 14-hour day. Along with this variation in day length is a correlated variation in monthly temperatures from the equator to the limits of the tropics. Another feature affecting tropical temperatures is cloudiness. Near the equator cloudiness is common, but it decreases toward the Tropics of Cancer and Capricorn (Richards, 1952).

With so much rain, the soils are well leached, tending toward the production of lateritic soils containing a mixture of alumina and iron oxide; the latter imparts a red color. The acid clay soil is often shallow, perhaps 3 to 7 feet, but may extend as deep as 65 feet (Aubert de la Rüe et al., 1957). The leaves and other organic debris are quickly decomposed, so that leaf litter is thin, and the humus layer beneath is only 1 to 1½ inches deep (Goodnight and Goodnight, 1956). Authorities disagree on whether this rapid decomposition is accomplished entirely by soil organisms (bacteria, fungi, algae, earthworms, ants, termites, etc.) or whether it is accomplished in part by chemical oxidation (Richards, 1952).

There are several features of the plant life of the tropical rain forest that are outstanding: stratification, presence of tall broadleaf evergreen trees, abundance of lianas, presence of epiphytes, buttressed trunks of larger trees, cauliflory, large numbers of tree species, and uniformity of foliage. The tropical rain forest shows little seasonal change, and plant growth occurs the year round. Most of the plants are woody, including the vines. Although the highest trees are tall, they are not as tall as the redwoods of California.

The forest is generally considered to be stratified, with the highest layer extending from 90 to 140 feet, the second from about 40 to 80 feet, the third from about 20 to 35 feet. Under this is a layer of shrubs and saplings, and finally there is a layer of herbaceous plants on the forest floor. These strata are not as obvious as one might at first expect, since one seldom observes a cross-section of the forest, and looking up from the ground does not afford the proper perspective. Instead, sample plots must be cut and the trees measured to verify stratification. In fact, although each stratum is often discontinuous with respect to the others, sometimes there is no break between strata, but merely a concentration of most crowns at different levels. The upper stratum usually forms an open canopy, so that its trees are sometimes referred to as *emergents*. The second stratum forms a closed canopy under the first, and the third also usually forms a complete canopy.

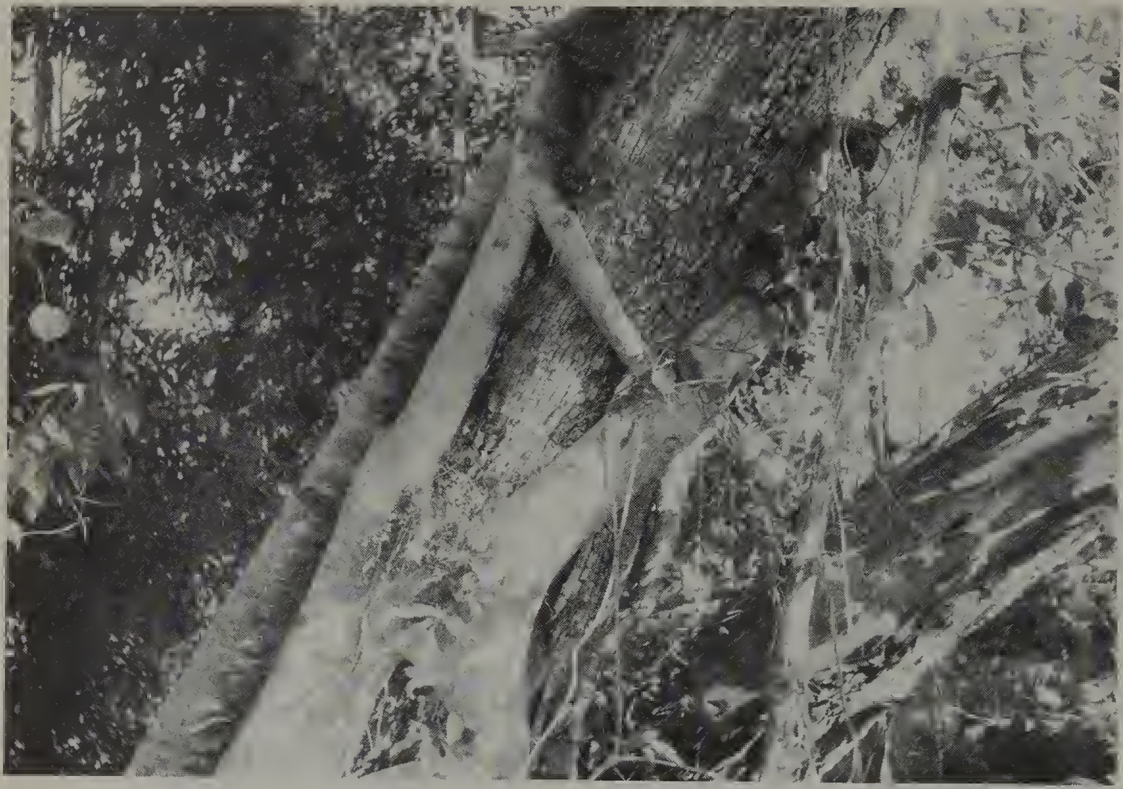
The dominant trees are usually of many species, so that one may have to hunt quite a distance for a second tree of one species. There are some rain forests, such as one on Trinidad, where a single tree dominates, but usually there are at least 40 and sometimes more than 100 species which will have trunks over four inches in diameter (Richards, 1952). Each stratum will have its characteristic species. However, the dominants will be components of each stratum, since even the shrub and first tree layer will contain saplings of the upper two layers. Not all dominant species, of course, reach the upper strata. Common trees in North American rain forests include mahogany, Spanish cedar, satinwood, mora, purple heart, sapote, rosewood, and figs.

The shrub and herb layers are not as dense as is often believed, except where the forest has been cut or otherwise destroyed in such a way as to let in light. In climax forests the shrub layer may cover 40 to 50 per cent of the ground, and the herb layer 60 per cent, as in Chiapas, Mexico (Goodnight and Goodnight, 1956). Often, patches of bare ground may be exposed. Herbs and succulent plants belonging to the families Araceae, Cyperaceae, Rubiaceae, and Bromeliaceae are common (Aubert de la Rüe et al., 1957). Ferns may also be abundant.

One of the notable plant types of the rain forest is the *strangler* (Fig. 5-28). Stranglers are trees which begin life as epiphytes but after many years become self-supporting. The seeds of strangler trees like *Ficus, Schefflera,* and *Clusia* germinate in a tree and then send roots down through the air or along a tree trunk to the soil. As they grow, the roots may encircle the trunk of the supporting tree and finally girdle and kill it. By then, the strangler may have grown big enough to support itself.

Lianas, or woody vines, are another type of plant characteristic of this biome. These plants, belonging to any of a dozen or more families including ferns, may climb even to the uppermost stratum of the forest and help to fill in the canopy. Some twine, some have tendrils, and some send roots straight down from upper branches. These vines may reach a diameter of 6 to 18 inches.

Another type of plant also grows on the trees but does not send roots down to the soil. These plants, *epiphytes,* must obtain all their moisture and minerals from the air, and so are sometimes known as air plants. The most common types

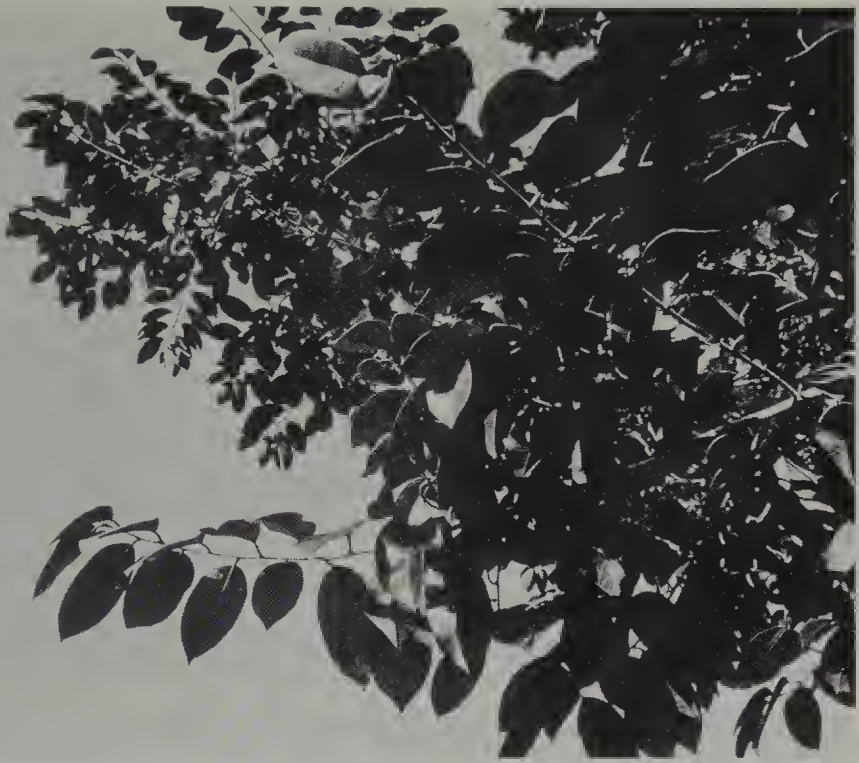


William E. Werner, Jr.

Fig. 5-28 Tropical rain forest features. A strangler fig will eventually girdle the larger tree. Epiphytic ferns are growing between the fig tree and its victim, while lianas drape alongside.

belong to the pineapple, orchid, milkweed, and fern families (Fig. 5-28). Algae, lichens, mosses, and liverworts are other types of epiphytes. They grow especially well on trees with rough bark. Air plants must be able to survive on low amounts of water, although some, such as the tank bromeliads (pineapple family), store water and in so doing provide a habitat for small aquatic animals.

A few other typical features of tropical rain forest plants are of interest. First is the fact that so many of the plants are woody. In fact, only a few herbs, vines, and epiphytes are not woody. Many plants familiar in temperate zones as herbaceous forms have woody relatives in the tropics. Another feature is the way that the trunks of larger trees appear to be strengthened by buttresses or winglike expansions of the bases of the trunks. Leaves are of course evergreen and tend to appear waxy. It has been noted that the ends of the



William E. Werner, Jr.

Fig. 5-29 Drip-tip leaves, another feature of the tropics. Here, the leaves of satin leaf, *Chrysophyllum olivaeforme.*

leaves have sharp tips. This feature is known as a *drip-tip* and probably leads to fast drying of the leaf (Fig. 5-29). The significance of this feature is a matter of controversy (Richards, 1952). Finally, many species tend to bear flowers directly on large stems or trunks, a phenomenon known as *cauliflory.*

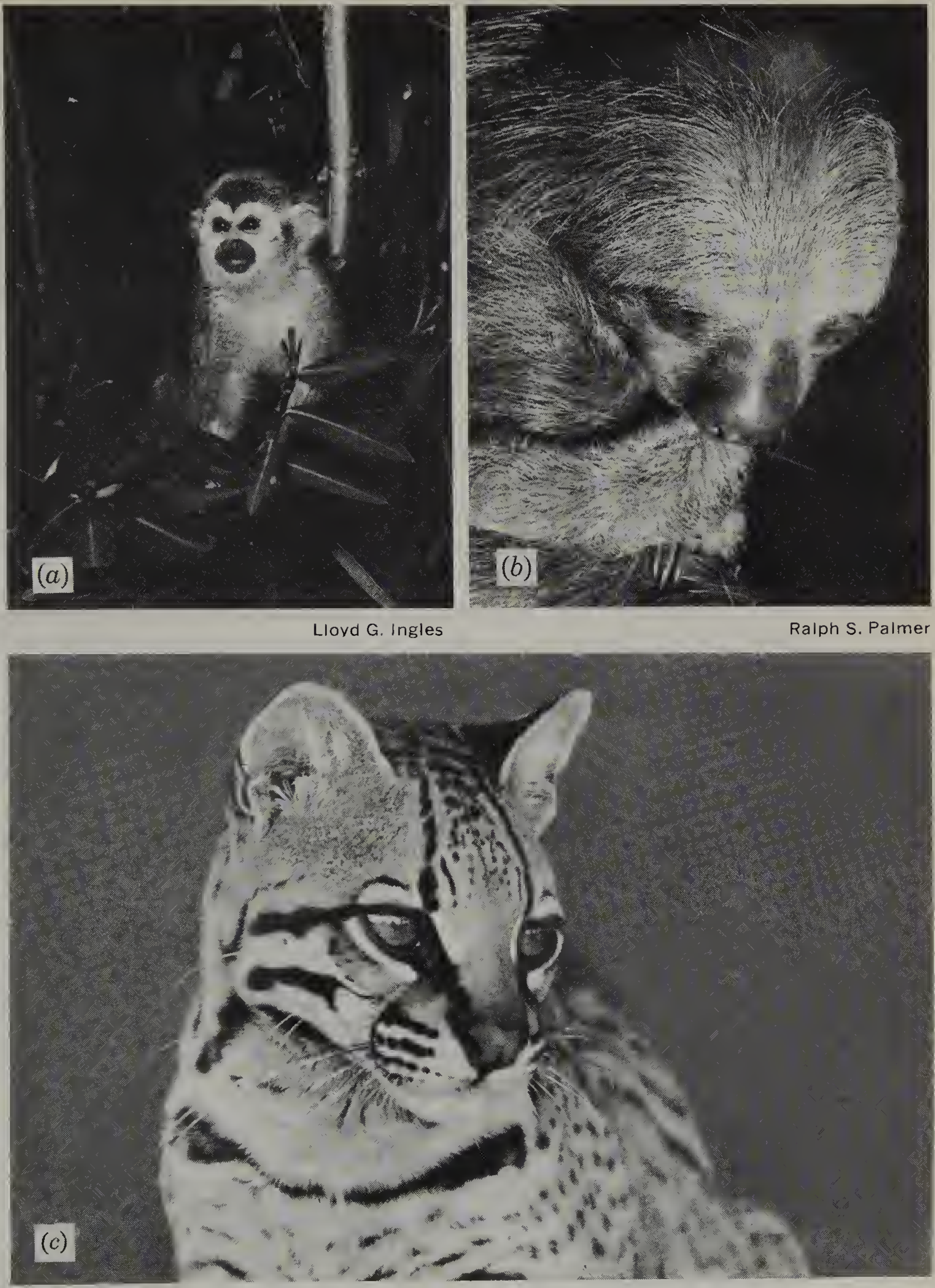
Despite the abundant trees and lianas which might provide homes for animals, the majority of the animals live on the forest floor (Allee, 1926*b*). It is perhaps the dangers of arboreal life and even more the constancy of the environment of the forest floor that are responsible for this fact. The stability of the forest floor environment is due to the insulation of the heavy foliage above. Allee (1926*a*), commenting on the extreme stability of the forest floor in Panama, wrote, "animals need only to avoid the higher temperature, light intensity and lower humidity of sun flecks on the forest floor in order to keep under air conditions so constant that they must excite the envy of any experimental ecologist with experience in trying to control environmental factors for land animals in the laboratory."

Of all animals, ants are probably the most numerous and conspicuous. The numbers present may vary with the season, and Goodnight and Goodnight (1956) suspected this was the reason for their finding only 407 animals per square meter during the dry season in Palenque, Mexico, as compared with an average of 714 per square meter in Illinois (see also p. 121). They also found only 32 animals per square meter on low-growing shrubs. Animals common in the soil included ants, earthworms, snails, mites, spiders, millipedes, beetles, termites, and insect larvae. Sweepings on vegetation revealed the abundance of ants, mites, spiders, leafhoppers, beetles, Hymenoptera, and butterflies.

Most of the animals are not restricted to one stratum of the forest, yet one can say that they may be more frequently found in one layer than in another. Some notable exceptions include termites of which some species may inhabit trees and the forest floor, others the forest floor and the soil beneath. Ants may range through several strata; some through all levels above shrubs (Allee, 1926*b*). Birds also tend to range from low to high trees. In the undergrowth, woodpeckers, bats, lemurs, lizards, and frogs may be found.

Snakes are not abundant. Allee (1926*b*), in speaking of the Panama rain forest, states that ". . . near Chicago, one sees more snakes in 100 yards in low prairie than in 2½ months in Panama." Other workers have made similar observations. On the other hand, numerous species of extremely poisonous snakes do occur here, such as coral snakes, fer-de-lance, and bushmasters. Interestingly enough, poisonous snakes are absent from most of the large islands of the Caribbean, although nonpoisonous snakes of many species are present (Ditmars, 1931).

Spider monkeys and howler monkeys may be seen and heard, but most mammals are conspicuous by their absence. Arboreal forms have special adaptations for their mode of life (Fig. 5-30). Many, such as the ocelot and squirrels, may have well-developed claws. Others, such as tree frogs, have sucker disks on the toes, while geckos and chameleons may have adhesive ridges. Opossums have opposable digits, and South American monkeys, such as the squirrel, howling, and capuchin monkeys, have prehensile tails to aid them in climbing.



Lloyd G. Ingles

Ralph S. Palmer

Ralph S. Palmer

Fig. 5-30 Mammals of the tropical rain forest:
(*a*) Squirrel monkey, *Saimiri orstedii.*
(*b*) Three-toed sloth, *Bradypus griseus.*
(*c*) Ocelot, *Felis pardalis.*

In the crowns of trees, birds dominate among the vertebrates (Aubert de la Rüe et al., 1957). Common canopy birds include hawks, trogons, vultures, toucans, grosbeaks, woodpeckers, and parrots. They share this stratum with sloths, monkeys, lizards, and frogs, as well as insects.

Of all the animals of the tropics, as elsewhere, insects are the most numerous. Aubert de la Rüe et al. (1957) list the following kinds of animals that have been found on Barro Colorado Island in the Panama Canal Zone: 2,000 insects, 306 birds, 66 reptiles, 58 mammals, and 34 amphibians. A greater variety of animals as well as plants occur in the tropical rain forest than in any other biome, but biologists do not agree on the reason for this fact. It may be due to shorter life cycles and consequently more generations per year, or a wider variety of habitats, or ideal living conditions which produce keen competition, or a combination of these factors, or other reasons. Invertebrates and cold-blooded vertebrates tend to be larger here than elsewhere, as seen in certain beetles, butterflies, and snakes.

In the tropics there are some interesting minor plant-animal associations. For example, some trees, such as certain species of Acacias and Cercropias, harbor stinging ants (Allen, 1956), while other plants may be hosts for other types of ants. Bromeliads are perhaps even more important as a place where animals which require water for their life history may live. Wheeler (1942) reported 342 species of animals from bromeliads, many of which were Diptera (mosquitoes, midges, etc.) and ants. In addition to the Diptera and ants, a wide variety of animals use the water trapped in the leaf bases of bromeliads as their pond in the sky, including worms, rotifers, snails, crustaceans, leeches, planarians, fresh-water crabs, and odonate nymphs. Laessle (1961) reported an interesting situation in these epiphytes, where frogs, *Hyla brunnea*, laid successive batches of eggs. The earliest eggs hatched out and used the later ones as their food supply.

Although the rain forest biome encompasses a considerable area, much of the tropics is occupied by other biomes. As rainfall decreases, one finds the presence of deciduous forests, savannas, thorn forests, and deserts. Or, as one ascends a mountain, he may leave a rain forest and enter a montane forest; and if the mountain is high enough, one may encounter alpine conditions and even perpetual snow on top.

Montane Forest

The montane forest biome may be found at elevations of about 2,000 feet up to nearly 13,000 feet (Aubert de la Rüe et al., 1957). It is probably the lower temperatures that produce this different biome. There is approximately a 1° Fahrenheit drop in temperature for every 300 feet one ascends. Relative humidity may rise with elevation until there is a continual cloud and drizzle.

The transition from rain forest to montane forest is gradual, with deciduous trees becoming increasingly more abundant. Near Golfo Dulce in Guatemala, Allen (1956) found a five-layered forest with 89 species of trees in the canopy and 207 in the understory below 2,000 feet. Above 2,500 feet, the forest had changed so that only one to four species dominated, including oaks, cedars (*Cedro* sp.), and stilt palms. Conifers may appear at elevations of 6,000 feet and higher in Mexico, Guatemala, and Costa Rica. Different species of pine, oaks, and firs dominate at various elevations to about 13,000 feet, at which height snow remains once it has fallen. From 13,000 feet to 15,000 feet alpine conditions occur. At about 15,000 feet there are daily frosts and permanent snow. These conditions are not common, for there are only three mountains in Mexico with elevations of 15,000 feet or more (Aubert de la Rüe et al., 1957).

Tropical Deciduous Forest

At lower elevation, as rainfall decreases, other biomes are found. Thus deciduous forests occur where there is a pronounced dry season. The trees in these forests may be of enormous size, but they are not as varied in species as in the rain forest. The majority of the trees are deciduous, and usually there are only two strata. Common species include mahogany, Spanish cedar, logwood, cocolobo, lancewood, Panama redwood, rain tree, possumwood, and silk cotton tree.

Tropical Savanna

In many areas where one might expect deciduous forest because of rainfall (from 40 to 100 inches a year), there occurs instead a savanna. Many students of the tropics believe that all North American tropical savannas or grasslands have a climate that could support either a deciduous forest, thorn forest, or desert. Thus Beard (1953) is quite emphatic in stating that the tropical savanna would not occur without the presence of fire or adverse *edaphic* (soil and site) conditions. He states that the vegetation is adapted so as to be fire resistant but does not depend on fire for maintenance of the community. Allen (1956) pointed out that extensive savannas are always found in areas of known high pre-Columbian populations.

The important and dominant group of plants of the savanna are herbs, especially grasses and sedges. Although trees, palms, and shrubs are often present, they may be absent. Beard (1953) classifies savannas into tall bunch grass, sedge, and short bunch grass according to the dominants present. The tall bunch grass type is the common one, with sedge savanna occurring in areas of high rainfall or wet spots and the short bunch grass occurring in small dry areas.

The terrain on which the savannas are found may be hilly or flat. They are found in low-lying areas of British Honduras and in the eastern part of Nicaragua, as well as on the Pacific side of Costa Rica and Panama, where rainfall is lower and a dry season occurs. Here deciduous forests and savannas occur side by side. In Cuba, Haiti, and Puerto Rico, savanna is the typical vegetation, most of the original forests having been destroyed since the coming of Columbus.

Thorn Forest

In semiarid regions of the tropics a biome occurs which is called a thorn forest, since many of the dominant trees possess thorns. The trees are about 10 to 30 feet high; although they may be sparse, there is no grass between them. The leaves, trunks, and twigs of some are coated with wax. Many are leafless except during the rainy seasons. Some, like mesquite, extend tap roots into the subsoil.

Tropical Desert

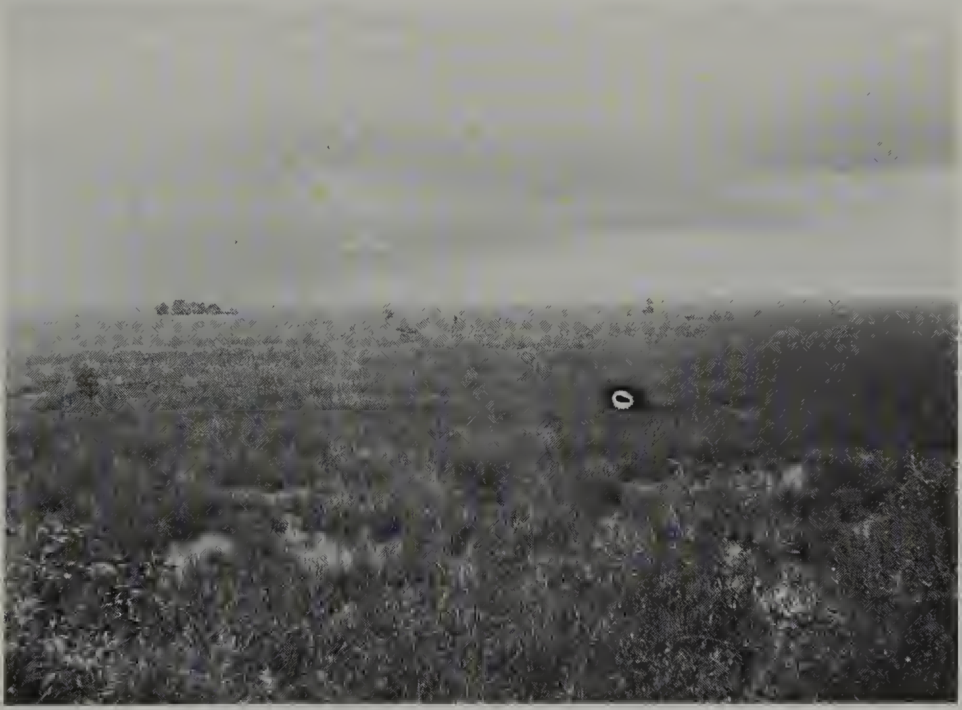
Finally, in the hottest and driest parts of the tropics there is a desert biome. Lower Central Mexico and the Netherlands Antilles have this biome. Temperatures may exceed 120° Fahrenheit, although the nights are usually cool. Vegetation is sparse, but some cacti may attain 60 feet. Yuccas, cacti, and other succulents are the dominant plants.

Southern Florida

Of interest is the southern tip of Florida in the biome classification. It has been classified as tropical, subtropical, grassland, savanna, and deciduous forest. Geographically, it lies entirely above the Tropic of Cancer. However, the warm Gulf Stream and its peninsular isolation give it an unusually warm, humid, and stable climate. Frost is rare, and rainfall is moderately high—about 60 inches a year.

The Everglades, which occupies much of the region, is essentially a broad and very shallow river flowing south from Lake Okechobee to the southern extremity of Florida (Fig. 5-31). The depth of the water fluctuates seasonally; during the dry season the mucky bottom of much of the "river" is exposed to the air. Saw grass (a sedge) grows in abundance, giving the area the appearance of a prairie. The prairie of the Everglades seems to be the result of fire and seasonal submergence.

On occasional higher ground are communities called *hammocks*. The vegetation of hammocks includes such rain forest features as broadleaf evergreen trees, drip-tip leaves, epiphytes, stranglers, and lianas (Fig. 5-32). The trees and shrubs include paurotis palm, royal palm, cabbage palmetto,



William E. Werner, Jr.

Fig. 5-31 The Everglades from Pa-Hay-Okee observation point looking northward. This picture was taken in late September, after a lengthy rainy spell, so that the water level of the "river" was high. Note small hammock to the left, on the horizon.

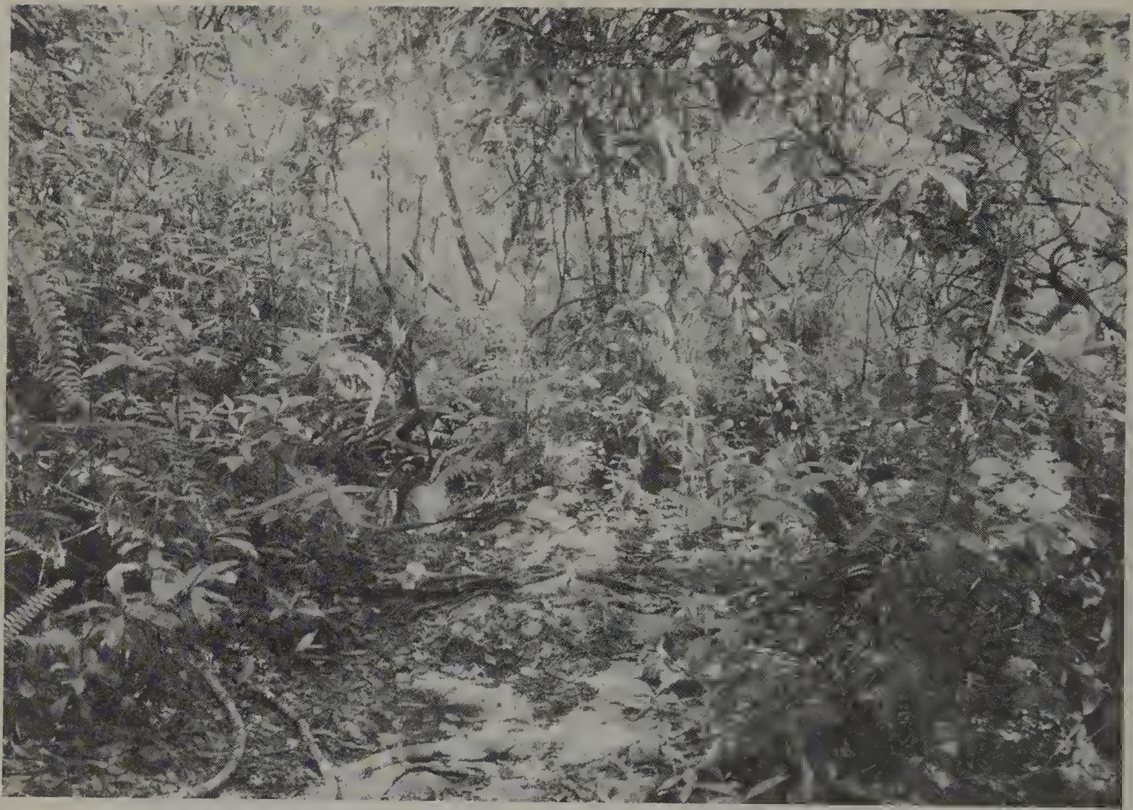


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Fig. 5-32 (*a*) Interior of a hammock, showing lush growth of ferns, shrubs, and lianas. This area was recently burned.

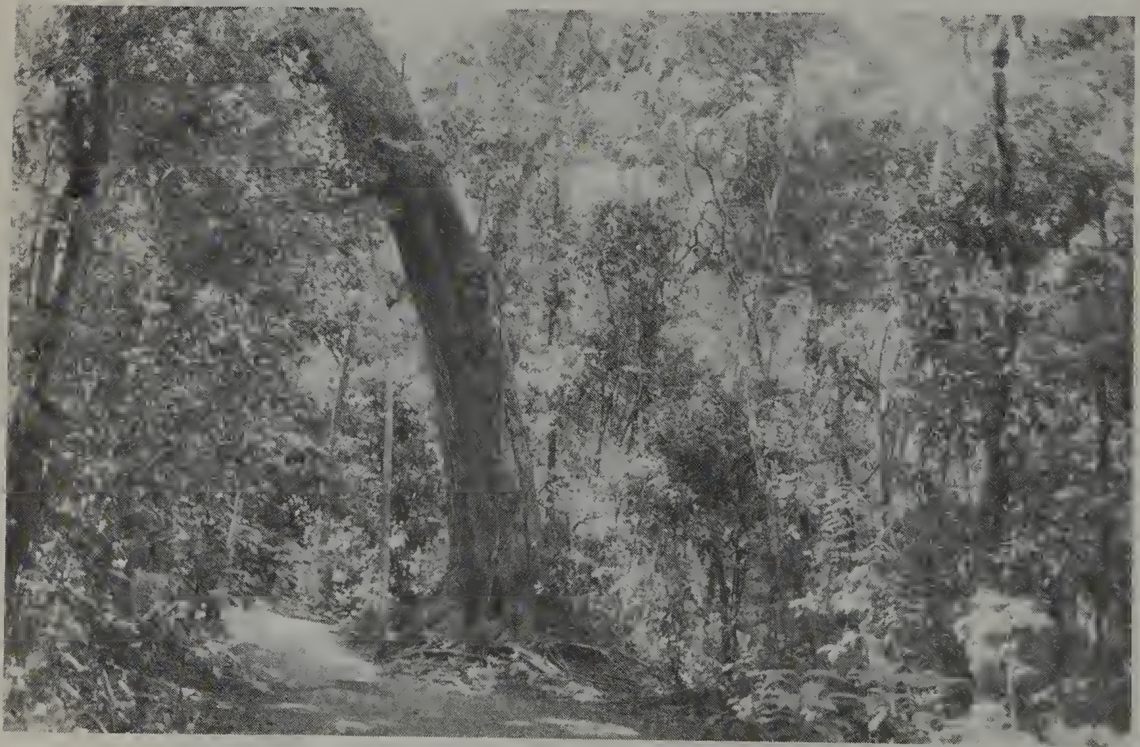

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Fig. 5-32 (*b*) Interior of a hammock, showing a few large trees and dense undergrowth. Gumbo Limbo trail of the Royal Palm hammock.

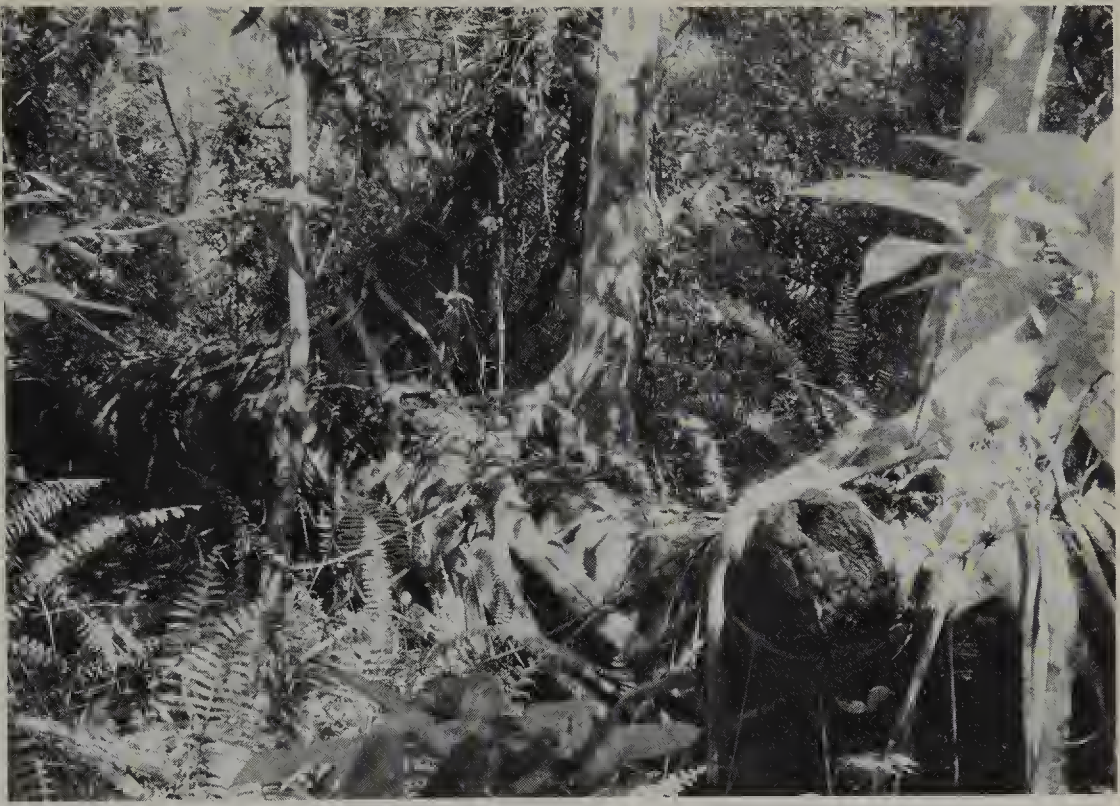

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Fig. 5-32 (*c*) Interior of a hammock, showing a tree felled by a strangler fig. Royal Palm hammock.

live oak, mahogany, satinwood, gumbo-limbo, strangler fig, lancewood, pigeon plum, and wild coffee. A vegetational analysis by Alexander (1958) of hammocks near Miami shows that of 43 species of woody plants, only 11 were of temperate affinities. Plants of West Indian affinities not only dominated in numbers of species but in percentage frequency and density.

The West Indian species create a tropical appearance, although the climate is not that of a tropical rain forest, nor is the vegetation structured like a rain forest. Complicating the picture is the fact that very few of the animals are tropical. The zebra butterfly, a brightly striped land snail, and a few birds, such as the ani and the white-crowned pigeon, are tropical, but on the whole the fauna is temperate.

Along the shores of southern Florida and the Florida Keys are mangrove forests similar to those of the tropics. The same four species are found and in the same ecological situations (Fig 5-33). The red mangrove grows out in the water on stilt roots. Closer to shore will be found the black man-

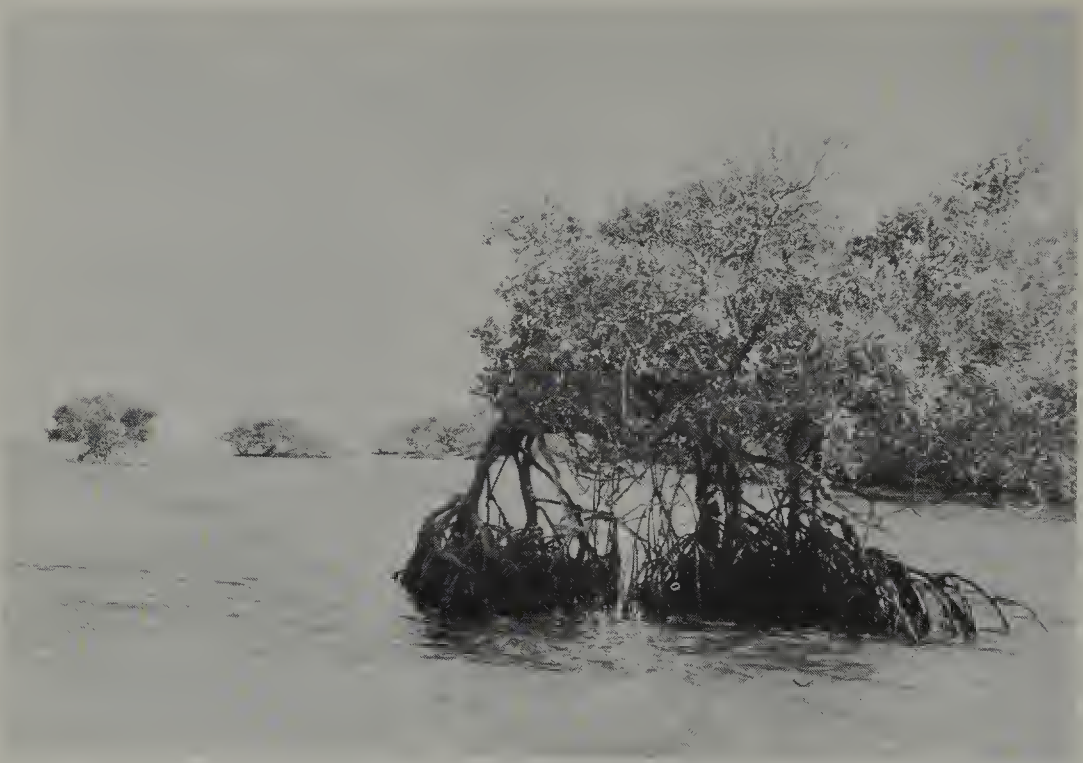

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Fig. 5-33 Mangroves on the south Florida coast. Red mangrove, *Rhizophora mangle,* with its prop roots, in foreground and extreme left background. Black mangrove, *Avicennia nitida,* to the right of red mangrove in background. *Avicennia nitida* lives near high-tide line and has numerous small pneumatophores which protrude above the soil surface.

grove with numerous pneumatophores which reach to the surface at high tide. Back on higher ground is the white mangrove, which may have a few pneumatophores, and buttonwood, which occurs above the high-tide mark. Much of the southern Florida coast is or was covered with this mangrove community. In the western and wildest part of the Everglades are untouched mangrove forests 100 to 125 feet high.

Thus, southern Florida seems to be an interesting transitional area between tropical and temperate biomes, more isolated from one component (tropical) than from the other (temperate) and in such a way that the isolation from the tropics is more effective against dispersal of animals than against dispersal of plants.

The preceding discussion of biomes considered only the major biomes, and only the general features of these. For example, part of the southwest is covered by a geographically small biome known as *chaparral.* Within each of the biomes are many variations in climax communities which could not be considered in this brief account. Furthermore, successional communities and lands planted in crops or occupied by human structures may occupy large areas of a biome. In some biomes, such as the grassland, it may in fact be difficult to find even a vestige of an original climax community. Here the only natural communities may be those which have been severely disturbed by man or nature and are in some stage of succession. In the next chapter we will consider such communities and how they may gradually return to a climax condition.

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chapter 6

Succession in terrestrial communities

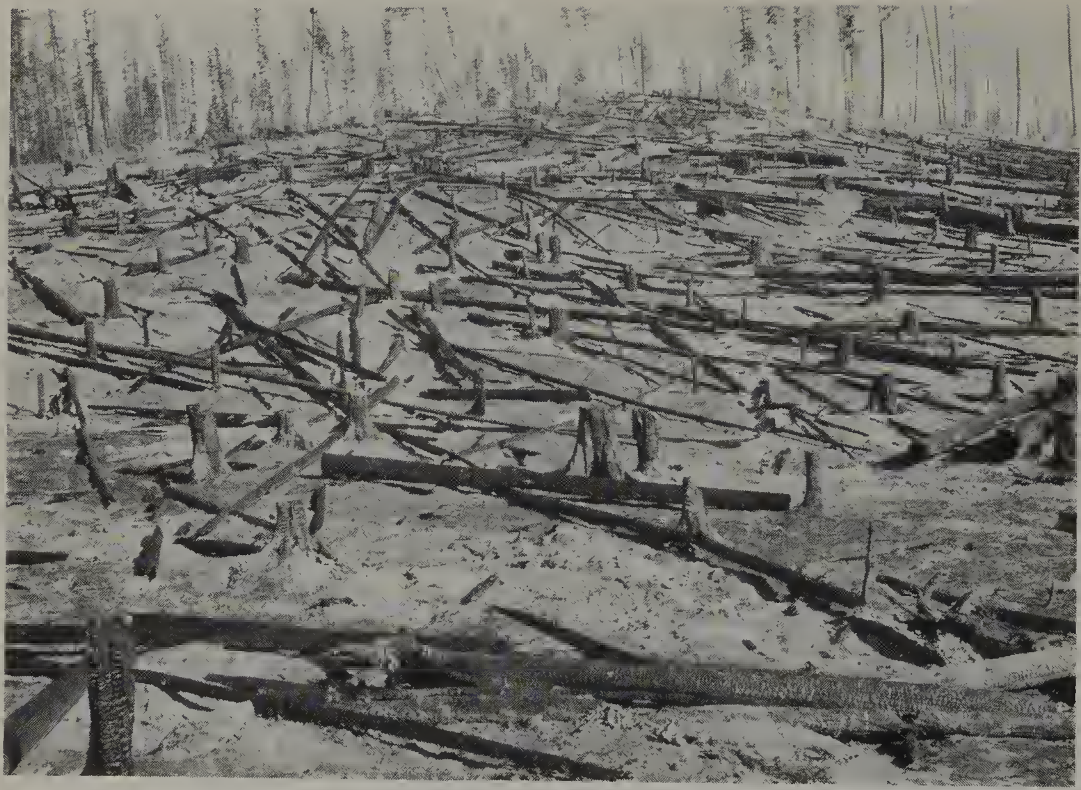
Although we speak of climax communities and think of them as large homogeneous areas in which the biota is relatively uniform, such areas are frequently difficult to find under our conditions of civilization. For example, in the forested biomes one seldom sees a vast, uninterrupted area of trees. There may be occasional bodies of water, such as lakes, rivers, and streams; or open fields planted in crops; or extensive areas where fire has recently leveled a woodland to charred ruins (Fig. 6-1). Even in the West, where animals and plants tend to be in a more natural condition over large areas, there are still deviations from the climax community in areas of extensive rock outcrops, overgrazed range, or salt flats. Such regions may have few organisms or may include a community unlike that of the climax type for the region. These departures from the climax type are frequently observed, a fortunate occurrence for the ecologist and field biologist; for the existence of such areas, as well as their origin, development, *For every wound the ointment of time.*

Welsh proverb

and fate, provides us with an opportunity to understand the dynamics and construction of climax communities.

If a person could watch these islands of nonclimax communities over a period of time, he would see them change slowly in the direction of the climax community. In some cases this would be a lengthy process, not observable in a man's lifetime. In other instances the change might be completed in a few decades. Careful scrutiny would reveal that the process of change follows a definite pattern. The movement of gradual, orderly, and predictable changes in the composition of communities toward the climax type is known as *succession.* There is some tendency, at least in certain instances, for succession to occur in steps, by definite, easily detectable communities. It is obvious, of course, that there must be transition periods, even in such instances, with perhaps the major steps lasting longer than the transition periods.

As we travel along a highway, the variations of a climax



Jack G. James, Soil Conservation Service, U.S.D.A.

Fig. 6-1 Woodland destroyed by fire, Kaniksu National Forest, Washington. Even the organic humus of the forest floor has been reduced to ashes.

community mentioned above are easily visible. These are the major variations. Upon closer inspection of the areas that at first glance appear homogeneous, one will usually find smaller variations. Perhaps there will be a boulder covered with lichens and moss in the midst of a forest, or a huge tree rotting away on the forest floor. In time, these smaller variations, like the larger and more obvious ones, will be obliterated in an orderly manner; ecologists consider them situations in which minute examples of the phenomenon of succession may be demonstrated. Such small variations are present in every community. An area undergoing succession may therefore cover square miles or only a few square feet.

It was mentioned that rivers, lakes, ponds, and other aquatic areas relieve the monotony of climax communities, and it was intimated that these variations, too, were only temporary. In a process similar to that occurring on land, aquatic communities change until an end point is reached, that point usually being the terrestrial climax community. The way in which aquatic communities do so, however, is sufficiently distinct to warrant separate discussion in a later chapter (see Chap. 7). Suffice it to say here that succession is occurring everywhere, and the process is basically the same in aquatic and terrestrial situations.

If succession proceeds from an area devoid of organisms, or from an area which has not been changed physically by organisms, it is called *primary succession*. If, on the other hand, succession proceeds from a state in which there are other organisms still present, or where their effects are still evident, as in an organically enriched soil, it is called *secondary succession*. All of the communities which are formed and destroyed until the climax community is reached are collectively termed a *sere*, and any one community of the sere is a *seral stage*. A primary-succession sere may, for example, commence with wind-blown sand and end with a prairie community. A secondary-succession sere may start with a plowed field where grasses had been growing and end also with a prairie community. The end point for both types of succession will be the climax community, whether it be desert, grassland, or forest. Only the origins of the two kinds of succession are different.

AGENCIES OF CHANGE

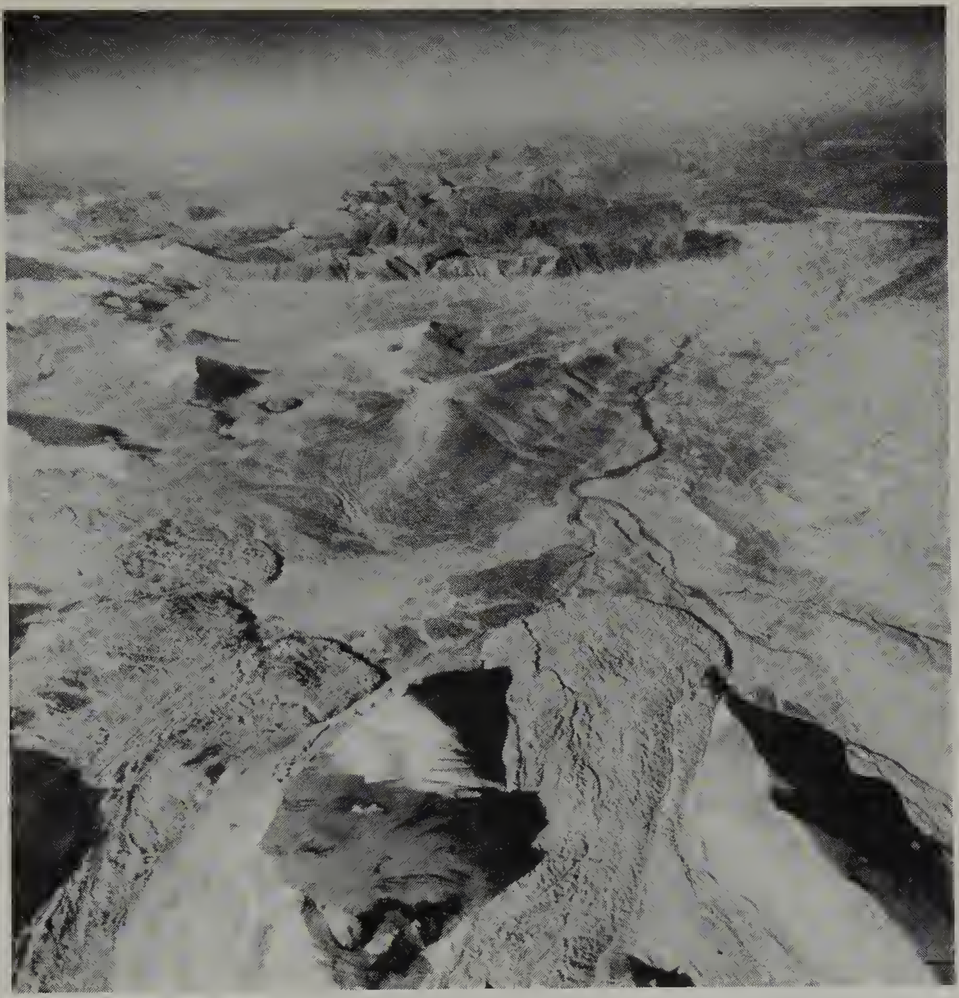
To a large extent, the dynamic state of communities of plants and animals, including the climax, is due to the multiplicity of agencies of change acting within them and upon them. Some of these agencies are physical, such as wind and rain; but the organisms themselves bring about many of the changes that are involved in succession. Some of the changes are destructive, tearing down a community to a lower stage or extinguishing life in an area altogether. Other changes are constructive. Both the constructive and destructive changes may be brought about either by biotic or physical factors or both. The tendency is that as soon as destruction of a community occurs, forces begin to work to rebuild it toward the climax state. This rebuilding process (succession) occurs through a gradual alteration of the species composition of the community as it is replaced by the next higher seral stage. The plants and animals, by their reactions upon the physical environment, such as in the accumulation of their wastes and remains, make the situation less favorable to themselves or more favorable to other organisms. In any case, certain species of a community are replaced by others until a new type of community is formed. In addition to these biotic factors, physical factors such as erosion by wind and water may help to bring about constructive successional changes in which certain members of one community are replaced by others.

Natural Catastrophes

Any physical phenomenon that will destroy life directly, or alter environmental conditions so that the old community cannot tolerate the new conditions, or allow new organisms to compete successfully with the old species, provides a situation in which succession may occur. Volcanic activity, earthquakes, fire, flood, glaciers, severe erosion, landslides, drought, and disastrous storms may temporarily denude an area or cause the death of many of the inhabitants, including dominants. When volcanoes erupt, their ashes and molten lava may kill all organisms for miles around. Topsoil is buried, and bare rock formed by the cooling lava must then be invaded by organisms. Katmai Peninsula in Alaska is still nearly free of vegetation as a result of the eruption of the Katmai volcano in 1912 (Fig. 6-2). Earthquakes and landslides may not be so drastic in effect as volcanic action, but they often destroy life in small areas.

Fire is a major cause of destruction of communities and often will cause deterioration of the site from the subsequent increased erosion. Many studies (Ahlgren and Ahlgren, 1960; Cook, 1959; Cooper, 1960; Hodgkins, 1958; Lutz, 1960*a*) have shown that fire has been prominent in the history of nearly all kinds of terrestrial communities. In some cases it destroys all life, in others it may destroy only a part of the community. Often, periodically recurring fires can determine the rate and direction of succession.

Floods may destroy life over large areas and deposit soil, gravel, and debris over existing communities. Although such regions are left without the larger flora and fauna, reoccupation is comparatively rapid, since soil remains in place and often includes organic nutrients, seeds, spores, or other living matter. The erosional deposits left on flood plains and changes in stream courses can be major factors in the final stages of succession toward a climax community (Hosner and Minckler, 1963).



Victor Cahalane, U.S. National Park Service

Fig. 6-2 The Valley of Ten Thousand Smokes, Katmai Peninsula, Alaska. The area is still almost completely denuded of vegetation as a result of a volcanic eruption in 1912.

In some disasters, destruction of the community is only partial. Drought may kill many organisms of a community but may leave enough individuals to retain its essential structure. Fires, windthrow (uprooting of trees by wind), and severe storms may kill only certain members of a community, but these catastrophes—and drought as well—may affect organisms such as trees which are dominant in the community. Lutz (1960*b*) reviewed the literature on the effects of windthrow, which leaves a pit where the roots are torn from the soil and a mound where the soil, roots, and stump are deposited (Fig. 6-3). Such a disturbance is relatively common in many forested areas and may allow shifting of the per-

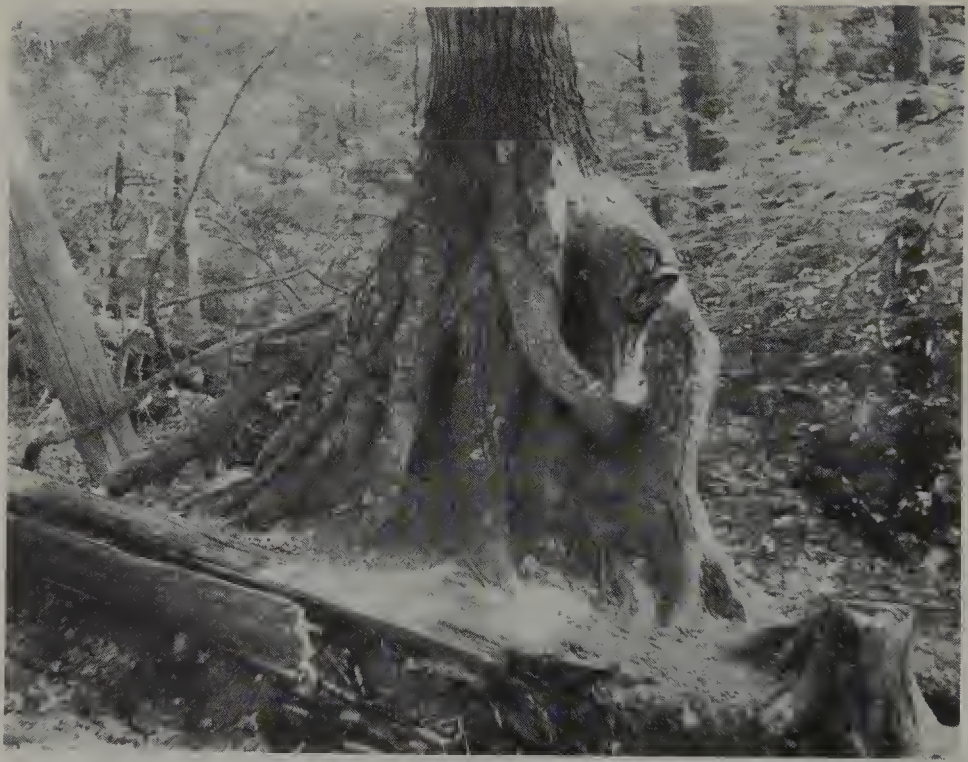


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Fig. 6-3 This tree started life on top of a mound caused by the windthrow of another tree. Harvard Forest, Petersham, Massachusetts. Often the remains of the windthrown tree are still present, and its species can be determined.

centage composition of the species in a climax community.

After a catastrophe has occurred, the changes through which the community will go are successional, and eventually the climax is once again established. By definition, these successions, in which some effects of previous life are left for new communities to build upon, are secondary.

In a sense, change of climate causes successional change, too, although in this instance a longer period of time is involved. In the recent glaciation of North America, not only was there a change of climate but the land under the ice was completely wiped free of organisms, and we may still witness the last stages of succession proceeding as a result of this destruction. This is certainly true of the ponds and lakes formed by receding glaciers, and it is also the case in boulder-strewn forests and perhaps even in the prairies of Canada (Coupland, 1961).

Changes in the Earth's Surface

In a similar way, rising and sinking of land masses may create changes which are so subtle that we do not recognize them as successional. Although movements of land masses occur gradually, they do produce conditions that are involved in succession. Thus elevation increases or changes drainage, which will have its effect on communities through different moisture conditions and in increased erosion. If the elevation is pronounced, temperature changes due to altitude will also be effected. Depression of land would bring about the same types of changes in environment as elevation, but in reverse. Furthermore, elevation or depression may raise land out of the water or inundate areas. It is believed, for example, that the weight of the glaciers on North America during recent geological history depressed the land so that an arm of the sea covered the area now occupied by Lake Ontario. Then, as the glacier receded to the north, the land was reelevated, a fresh-water

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Fig. 6-4 Some of the Thousand Islands in the St. Lawrence River, New York. This land is said to be rising and may eventually cut off the Great Lakes from the sea.

lake was formed, and the St. Lawrence River was established as an outflow for the Great Lakes. But the land is still rising, and it is believed that eventually the region of the St. Lawrence River known as the Thousand Islands (Fig. 6-4) will be dry land. Thus, organisms in this region will have changed from marine to fresh-water and finally to terrestrial. A slow succession will have occurred in which the elevation and depression of land is the causative agent.

Biological Agents

The interaction of organisms may often disrupt a climax community or alter the path of succession. For example, Skau and Day (1959) found that deer and beavers were instrumental in a rapid propagation of aspen and balsam poplar on a man-made island, because the feeding of the animals on these species caused the production of abundant suckers. Birds may hinder natural seeding, especially in coniferous forests such as that studied by Hagar (1960). Spruce budworm and other insect pests are considered important animals of the taiga because of the disruption they may cause in the climax forests of the north.

Man occasionally introduces a destructive organism by which the constitution of the climax community will be altered. The American chestnut was one of the dominant trees in the forest biome of eastern North America in the early days of this country. Then a fungus, the chestnut blight, was accidentally brought in, and in less than half a century the species was almost completely wiped out. Not only was the space formerly occupied by these trees left vacant, but their destruction has changed the interrelationships of other organisms in the community. What happened in this instance has happened many times when an organism is introduced into a new area. The introduction of rabbits and prickly pear into Australia, or of goats on oceanic islands, has disrupted the climax communities of those places. Finally, man with his plow, ax, fire, and bulldozer alters communities and creates situations in which succession may proceed.

THE PROCESS OF SUCCESSION

First Physical Changes

As soon as the destructive forces have finished their action, the constructive processes of succession begin. Again, the agents of construction toward the climax community are both physical and biological. Let us take, for example, bare rocks such as those left after a glacier has receded or after a volcano has erupted. At first, the only factors that may change the nature of the surface of the rocks are the elements. Rain and snow may now begin erosion. Rain as it falls through the atmosphere gathers carbon dioxide, and this in combination with water forms carbonic acid, which may aid in erosion. If a crack or fissure is formed, water in it may freeze, expand, and help to split the rock further. Stone particles carried by water act as abrasives and wear down the rocks, while the stones themselves are worn down by the contact. Wind, bearing small particles of sand, buffets against the rocks, helping to rub off small fragments. In parts of the western United States, the effects of wind erosion are pronounced, and softer rocks are worn away, leaving the harder ones standing out in relief (Fig. 6-5). Some of our most scenic national monuments feature this type of eroded rock.

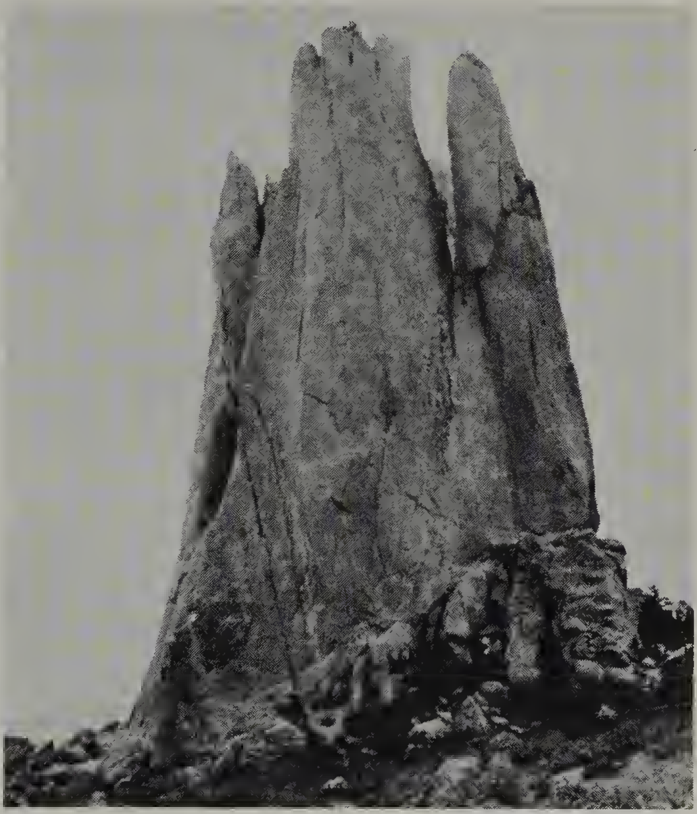

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Fig. 6-5 Wind-eroded rock, with the softer rocks worn away and the harder rocks remaining to form the peculiar shape.

Physical Effects of the First Organisms

In many biomes, however, such rocks do not long remain without a cover of organisms which will aid in the constructive processes. Spores of algae and fungi come through the air from surrounding areas, and soon algae or those sturdy symbiotic combinations of algae and fungi called lichens, are established on the surface of the rocks (Fig. 6-6). Thus wind not only erodes the rocks physically but transports biotic agents of erosion, for the lichens or algae in their growth will produce more carbonic acid. As they cling tenaciously to the rocks, they will tend to hold water on the surface and bits of stone that are chipped loose or blown there from another place. In this manner, with the coming of the plants, soil starts building up slowly but surely. Moisture can now be retained for a longer time, allowing greater periods for the processes of solution to work. This plant growth represents the first stage of a primary succession. From this point on, because of the

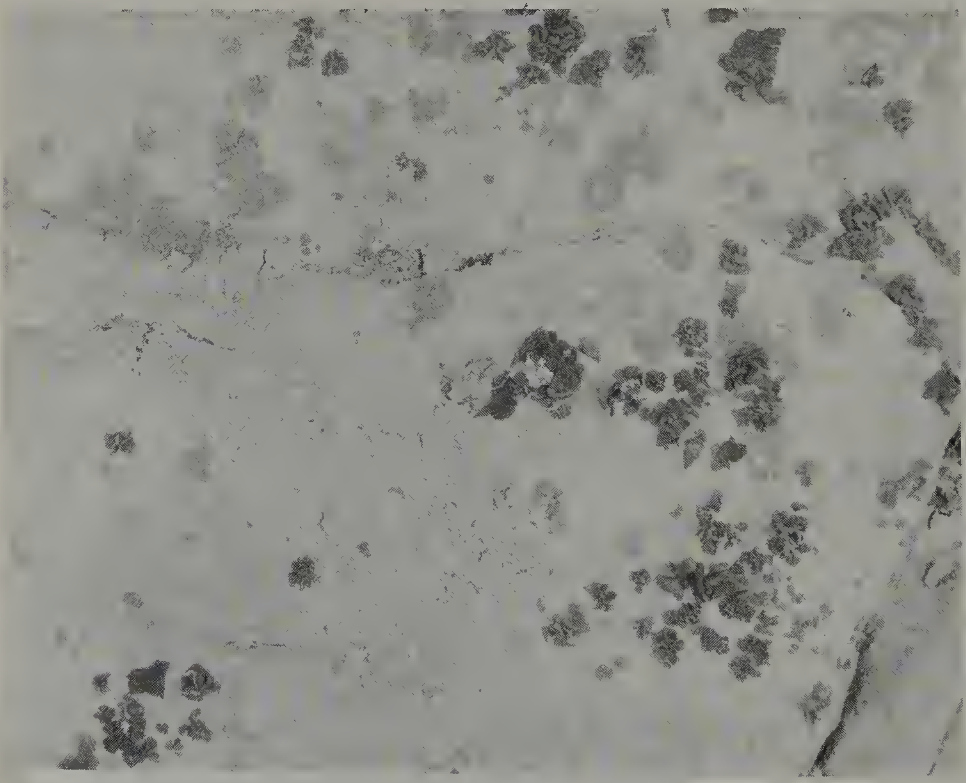

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Fig. 6-6 Pioneer plants (lichens) on a boulder in the coniferous forest biome.

plant cover, the rocks are more fully protected from the abrasive action of wind and sand and direct action of rain. One means of soil formation is thus limited. However, the action of the plants themselves in corroding the rocks, in splitting them with roots, and in the enrichment of this soil with organic matter from their dead bodies more than compensates for the protection they give. Hence organisms contribute a great deal toward the building of soil and therefore to the process of succession. There is, however, more to soil building than the work of wind, rain, and decaying plant matter, as we have described it here.

Pioneer Organisms and the First Stage of Succession

A sere on a bare area begins, as we have seen, with primitive plants. A bare area may be a sand dune, a clay bank, a gravel pile, or a rock. For our purposes, however, we shall continue our consideration of the principles of plant succession as it would occur on rocks, realizing that the details might be different if the habitat were different at the beginning. It is evident that only certain kinds of organisms can invade bare areas. Conditions on the bare rock are particularly stringent. Water on its surface is overabundant while it is raining but scarce or absent between storms. The sun heats the rock to high temperatures during the summer, but during the winter it may be covered with ice. There is no place for roots to grow for anchorage, so that an ordinary plant would soon be blown away by the wind, even if it could find a spot suitable for germination. Without plants, most animals find such an area inhospitable for invasion, for plants provide food and cover for them. Large animals like foxes or birds may make their homes in rocky areas, but even they must go elsewhere for food.

Plants such as lichens that may first invade an area ready for succession are called *pioneer plants*. They must be tolerant of severe climatic conditions and largely self-sustaining. They must be able to undergo long periods of adverse conditions to be able to take advantage of favorable moments for growth and reproduction. It is possible that some pioneers may not only tolerate these severe conditions but may require them for their existence. Thus certain mosses are found to be pioneers in situations where there is abundant moisture. Such moisture is necessary for their life cycle in order that fertilization may occur, for the sperm must swim to the egg in these plants.

Strangely enough, plants that are so tolerant of physical conditions of the environment are quite frequently intolerant of other organisms. In the case of the bare rock sere, we may assume that the pioneers were lichens. They have helped to corrode the rock and have perhaps collected some wind-blown soil. They, and any accumulated soil, maintain better moisture conditions, so that different kinds of plants may become established. One of the major mechanisms of succession is at once demonstrated as the next stage begins to develop; namely, that each community produces new environmental conditions which allow organisms less tolerant of severe climatic and environmental conditions to take over and eliminate the species of the existing community. The new invaders, profiting, in this case, by the gains made by the lichens toward soil formation, may crowd out the pioneer plants. We assume for the purposes of discussion that these invaders are mosses which were unable to invade bare rock (Fig. 6-7).

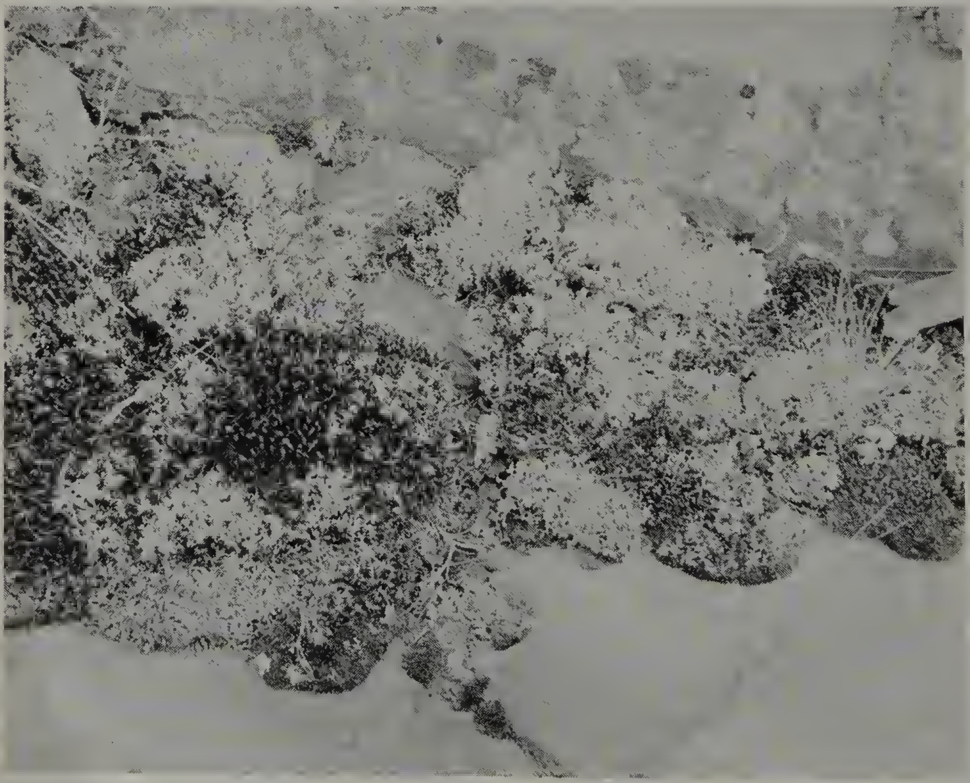

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Fig. 6-7 The lichens are being crowded out by mosses, which benefit from the soil prepared by the lichens.

The Moss Stage

In the early period of succession, there is still another obvious difference between stages, and that is complexity. As each succeeding stage develops, larger numbers of species are involved. The mosses which succeed the lichens may develop a dense cover, which will attract insects and other small invertebrates. These animals, like the mosses themselves, require more moisture than could be secured while the lichens were dominant, as well as food and cover which the lichens did not offer them. The smaller animals may attract some vertebrates as predators, such as the tiny insectivores, shrews.

The mosses continue to build up deposits of organic matter and soil as more rock is etched and broken away and as the old mosses and lichens die. The most significant change that these organisms can produce in an environment is that wrought by their own dead bodies. Throughout life they have taken in and accumulated in their systems salts, water, gases, minerals, and other compounds. Many of these substances have been synthesized into complex organic compounds such as fats, carbohydrates, and proteins. When the organisms die, they deposit these concentrated materials in the soil, and the products of their bacterial decay are instrumental in enriching the soil.

As the humus (decayed organic matter) accumulates, erosion of the rocks may slow down, although minerals are still leached from the soil and find their way eventually to the sea. Geologists believe that the saltiness of the oceans is due in part to this continual leaching process.

Probably the factor which is of most importance in succession is competition. Because of the changes wrought by the old community, new species are able to compete with the old species for space. In the new environment, the new species are more successful than the ones whose places they have usurped. Thus the lichens pave the way for the mosses, and the mosses may eliminate them. The mosses further contribute their products to the environment and improve it to the point that other plants may then successfully compete with them (Fig. 6-8).

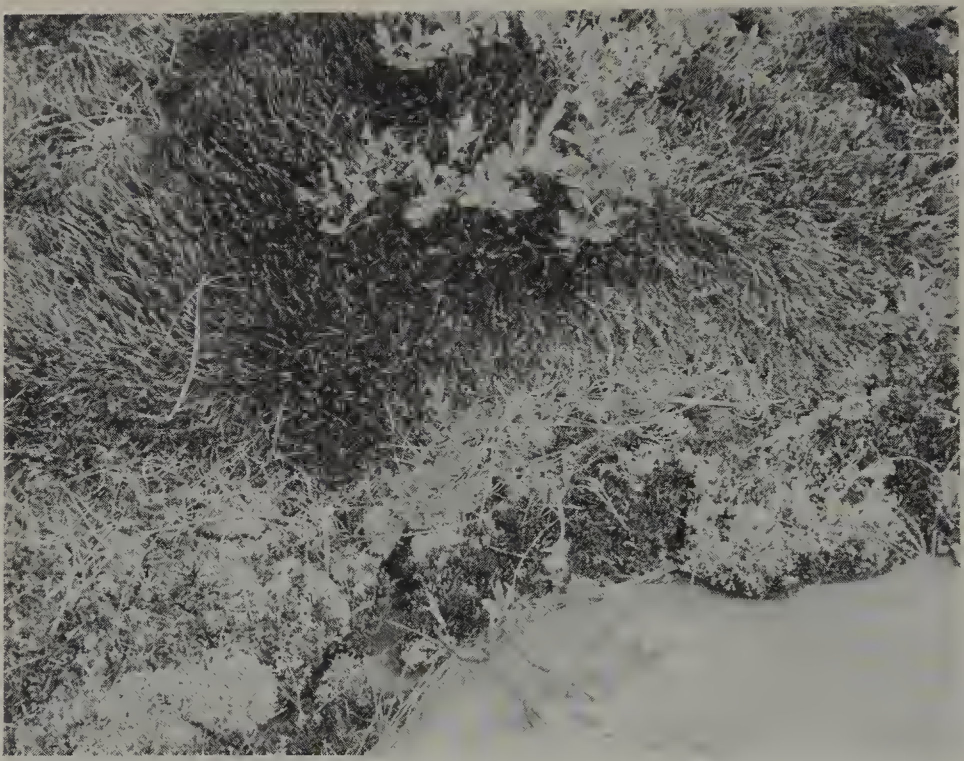

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Fig. 6-8 Invading grasses, weeds, and small shrubs are beginning to overrun the mosses.

The Herb Stage

Assuming that the rocks now covered with mosses are in an area where the climax vegetation will be a deciduous forest, the next invaders or competitors with the mosses may be large annual herbs such as goldenrods, asters, evening primroses, and milkweed, as well as a variety of grasses and other weeds (Fig. 6-9). In wetter areas, sedges of various species may predominate, along with water hemlock, blue-eyed grass, and rushes. In dry situations, where succession may proceed more slowly, plants such as poverty grass may be the only serious competitor of moss in this stage. Insects, usually quite abundant in the herbaceous stage, are the principal types of animals in the community. Especially numerous are grasshoppers, beetles, bugs, bees, and ants. During the summer many species of flies and butterflies are also to be found. Perhaps attracted by this source of food are the shrews and moles, while meadow mice find ample food in the grass, and jumping mice also make their homes here. Snakes of various kinds, includ-

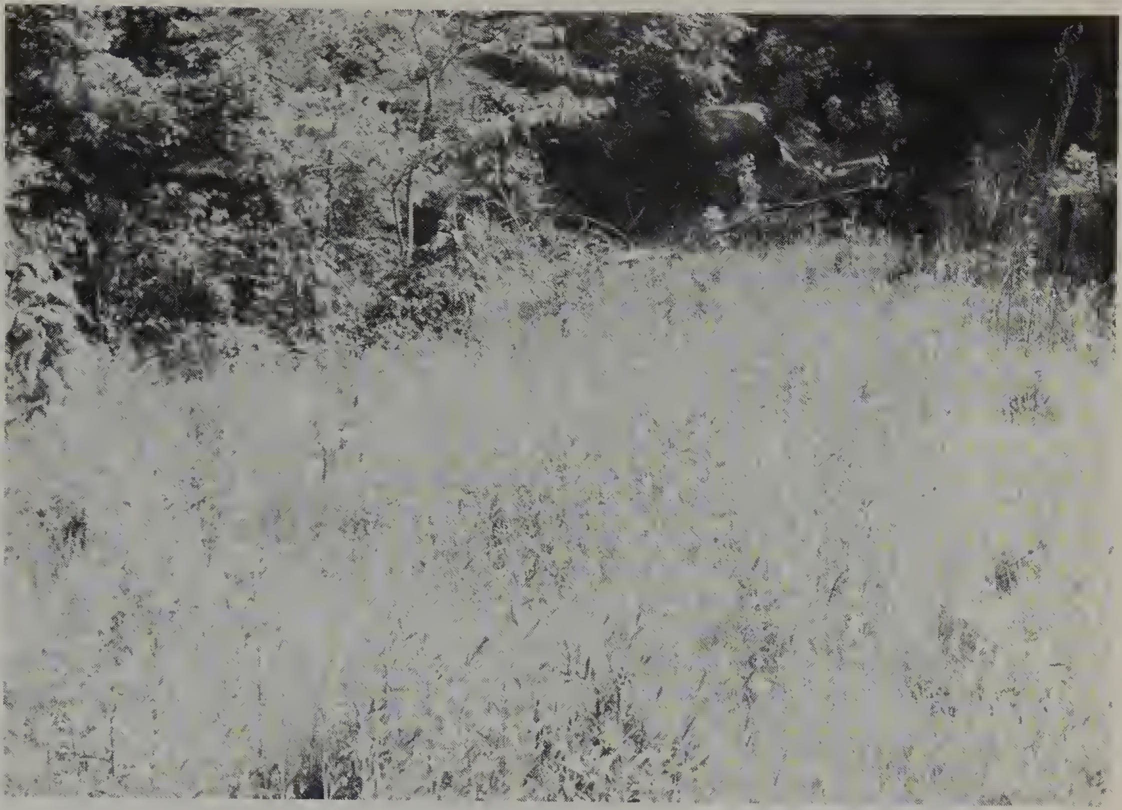

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Fig. 6-9 The herb stage. Milkweed, evening primrose, white snakeroot, and goldenrods are among the prominent plants.

ing the garter snake, ribbon snake, green snakes, and DeKay's snake may be found preying on the insects, earthworms, and other invertebrates, while such others as the milk snake, king snake, and blue racer survive in this habitat as predators of the small mammals. Larger mammals that also may be found in this community include rabbits, woodchucks, gophers, and ground squirrels. It should be understood that this prolific assortment is not always present in every herbaceous community. Especially in drier situations, mammals and reptiles may be few or lacking, and certain of the burrowing mammals require particular types of soils for their tunneling. However, there are other animals which may be temporary visitors. Many species of birds come here to seek out the insects, and some, such as the killdeer and several species of sparrows, nest here. Certain amphibians, particularly the meadow frog, are found where sufficient moisture is present; and larger mammals, such as deer, foxes, skunks, weasels, and opossums seek food in the meadow.

The Shrub Stage

Among the various herbaceous plants, the saplings of trees and shrubs will begin to grow (Figs. 6-10, 6-11). Just as mosses and lichens provided conditions under which the herbaceous plants could grow, so the grasses now do the same for the woody plants. The soil has been further enriched, the taller plants furnish shade and act as a windbreak, and the moisture conditions of the soil and the air just above the surface are improved. In general, as succession proceeds, the tendency is for the environment to become more *mesic*, that is, moderately moist. Thus wet areas will become drier and dry places wetter.

As the shrubs grow taller, they will become the dominant plants. This means that some of the plants of the herbaceous stage will not be able to survive. Sumac, aspen, poplar, blackberries, hawthorn, black locust, red cedar, white cedar, juniper, and mulberry are all examples of shrubs or small trees that may be prominent at this stage (Fig. 6-12). Usually only a

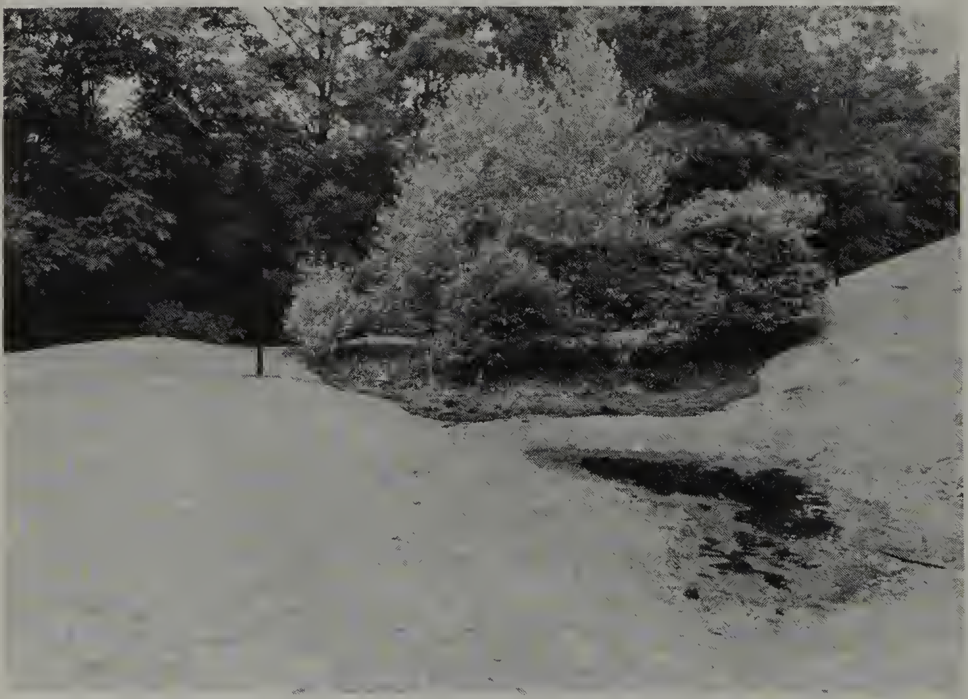

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Fig. 6-10 An island of vegetation in the midst of a granitic rock outcrop in Rhode Island. Enough soil has accumulated to allow the growth of trees (gray birch) and large shrubs. Note the rain pool in the foreground and the lichen cover on the rock.

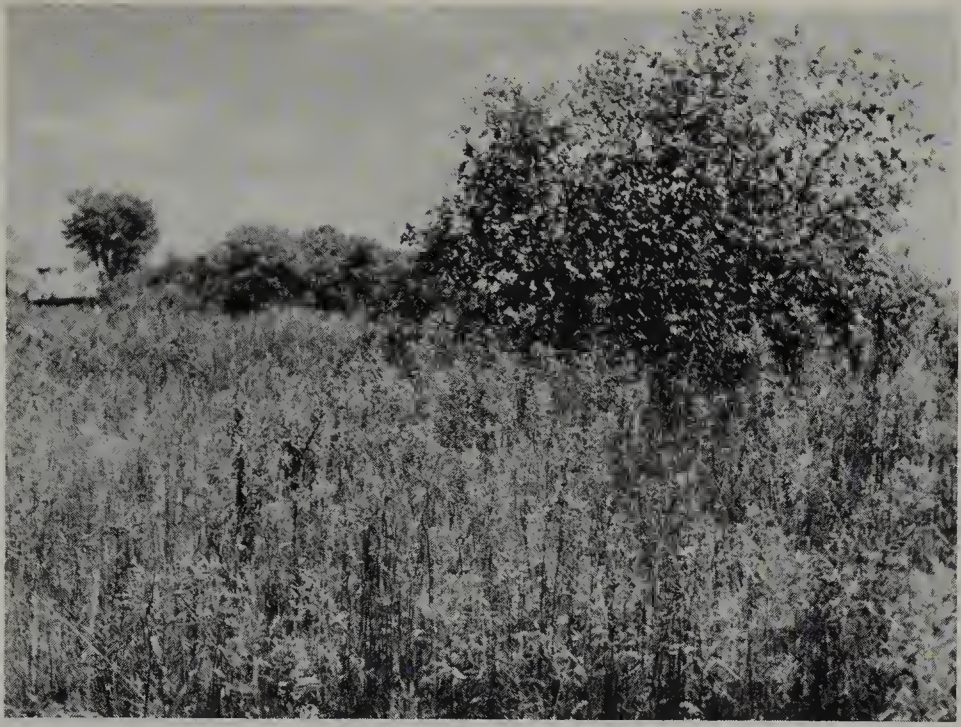

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Fig. 6-11 Beginning of the shrub stage. Here, alders and viburnum have started to invade the herb community.

few of these species will be present in any one location, the species being dependent upon several conditions including drainage, rainfall, original rock type, and the vagaries of distribution. Sometimes one species may predominate, even to the exclusion of all the others (Fig. 6-13). Saplings of trees may also be found in this stage, including maples, elms, pines, and oaks. Some trees are able to establish themselves along with the shrubs, while others are not able to gain a good foothold except in the shade of previously established plants. The shrubs may drastically reduce the number of herbaceous plants, and since the latter furnish the food for many of the insects and their predators, such animal forms are reduced in numbers. But while some animals may be fewer, others become more abundant. Especially numerous in this seral stage are birds, which use the shrubs for cover and often for nesting sites. Blackberries, mulberries, spirea, dogwoods, and viburnums may provide food as well as cover, and the birds, feeding on their fruits or seeds, may further distribute these shrubs by voiding undigested and viable seeds in their feces.

Frequently the herbs during this stage are so reduced in

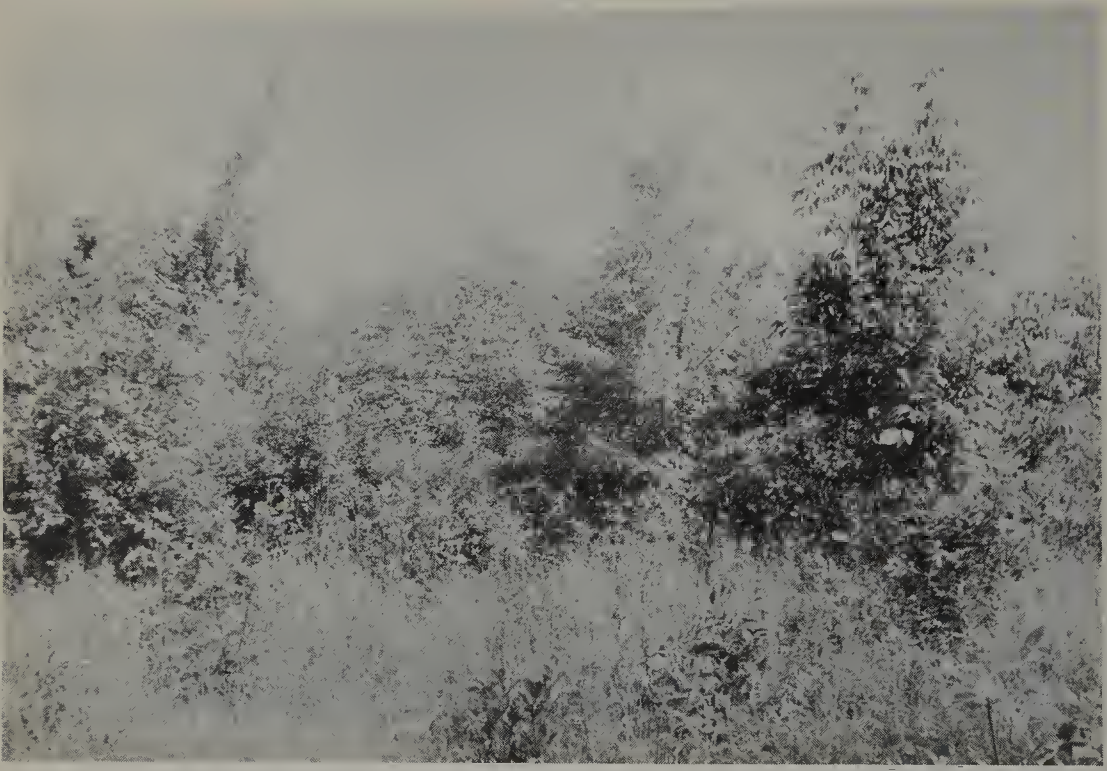

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Fig. 6-12 Shrubs and saplings are now dominant, the grasses and herbs having been reduced in numbers and importance.

number that insects and herbivorous mammals become quite scarce. Shrews, moles, and a few mice may be the only small mammals of the herbaceous stage still to be found. However, new species may now enter, perhaps because of reduced competition or the food and cover available in the altered surroundings. The white-footed mice and chipmunks may be among the newcomers in many parts of the country. The predators noted in the herbaceous stage are less likely to be encountered among the shrubs, for the supply of food in this community is not so abundant. Certain birds prefer this habitat to others, and nesting species may include towhees, song sparrows, goldfinches, catbirds, brown thrashers and yellowthroats. Martin (1960), in a study of succession in the taiga, found that the species of birds present, their abundance, and vertical distribution were characteristic of each seral stage studied, from pioneer to climax communities.

The kinds of soil in any area may affect the course of succession. Not all herbaceous plant stages are alike, and not all shrub stages are identical, even under similar climatic

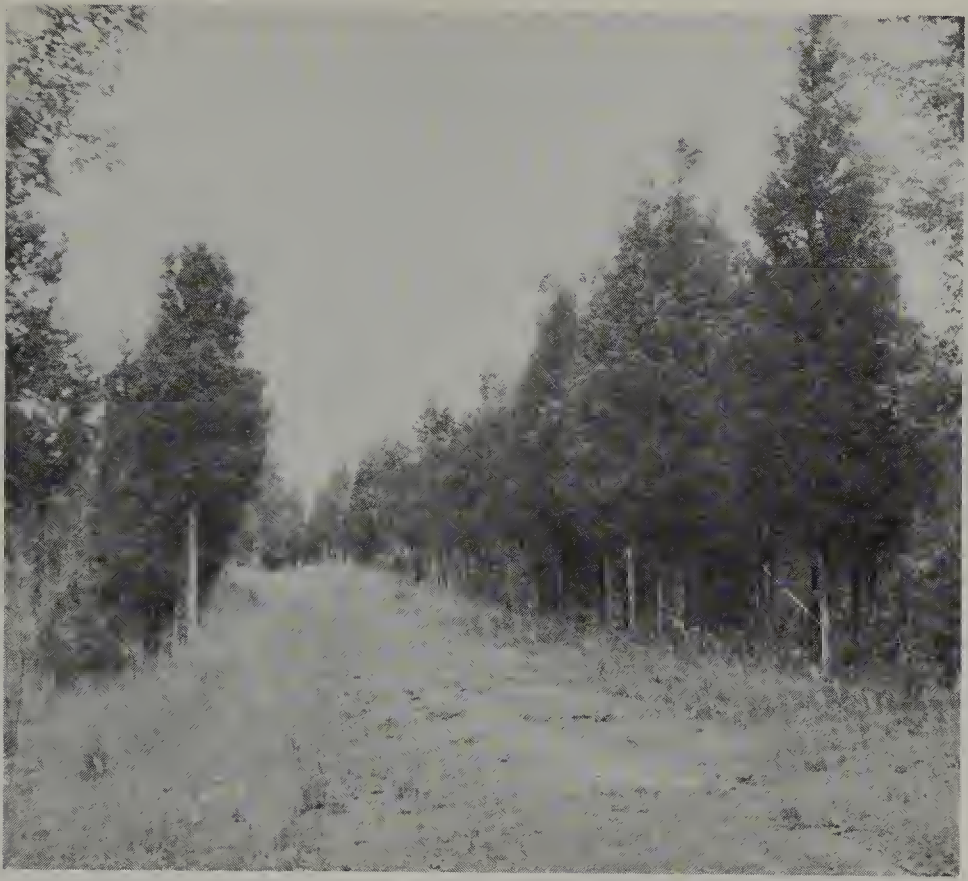

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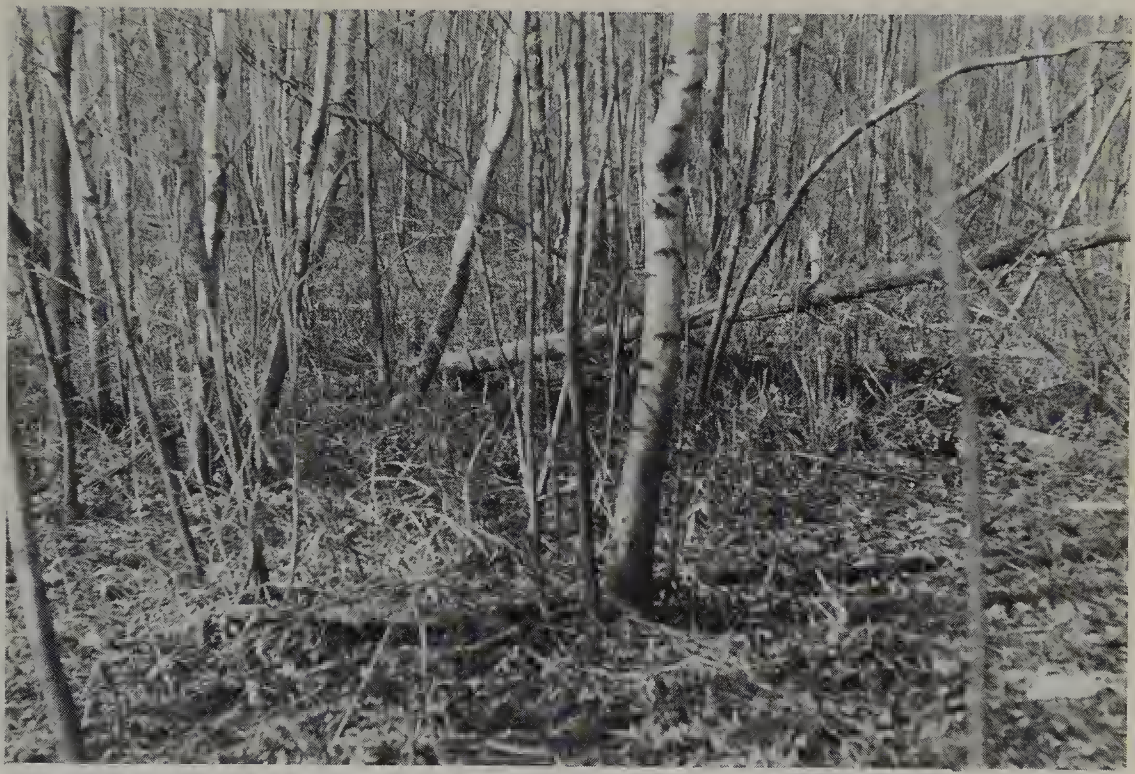
Fig. 6-13 Red cedars, *Juniperus virginiana,* dominate the shrub community over original limestone rock.

conditions. This is due to the different conditions under which a sere may start. One of the major physical differences which may affect the type of soil produced at first, and thus the types of plants which will occur there, is drainage. In moist, poorly drained areas, organic material as it decays tends to produce weak acids. Even if the original rocks were alkaline, the condition may be neutralized and an eventual acid condition will prevail. This may be unfavorable to bacteria, insects, and other organisms that normally decompose the organic remains. Therefore, organic materials remain on top of the soil and are not incorporated into it. In well-drained areas, the organic material may be washed away before it has a chance to become a part of the soil, while in more mesic conditions, organic matter has an opportunity to be converted into chemicals which may be mixed with the soil by earthworms, burrowing animals, and water. Many of these chemical end products may then be leached away, along with some of the mineral particles which the plants have dissolved from the rock, but the soil in the meantime has changed considerably.

An important aspect of soil formation is the development of soil fertility. It has been well known for some time that various species of legumes may harbor root nodules in which there are bacteria capable of fixing free nitrogen of the air, thereby making nitrogenous compounds available to plants. More recently, an unusual instance of nitrogen fixation was discovered at Glacier Bay, Alaska, on the site of a recent glacial retreat. Here, pioneer plants were a sickly yellow and grew poorly until two particular species invaded. These species, Sitka alder and Drummonds dryas (neither are legumes), have the ability to fix nitrogen through actinomycetes or other fungi in root nodules. Some of the fixed nitrogen leaks into the soil, but most of it is incorporated into the protoplasm of these plants, allowing the plants to grow rapidly. According to Lawrence (1958), alder thickets five years of age and five feet tall add through the nitrogen accumulated in their fallen leaves 140 pounds of nitrogen per acre to the soil each year and probably much more as they become older. The ability of pioneer or early stage succession plants to add such a vital plant nutrient to the soil is significant.

The Tree Stage

As the shrub stage ages and the sapling trees within it mature, the differences of soil and drainage that may have been present at first are reduced. In poorly drained areas, red maple, willows, and cottonwood may become the dominants in the first tree stage. In more mesic situations, this stage may include paper birch and white pine, while in well-drained and dry locations, aspens, gray birch, and cottonwood—or oaks, hickories, and locusts—may be found (Fig. 6-14). Shrubs from the earlier shrub stage may continue to exist as before, but now in a secondary role. Plants that cannot tolerate great amounts of sun begin to establish themselves under the trees, which soon form a complete canopy over them. Mosses, lacking the competition of the grasses, again become common, and ferns make their appearance, especially in the mesic and moist situations. As trees die and fall to the ground and leaf litter accumulates, fungi become abundant, and certain insects, including ground beetles, carpenter ants, wasps, bees, and flies may be found. Earthworms, millipedes, centipedes, sowbugs,



R. C. Axtell

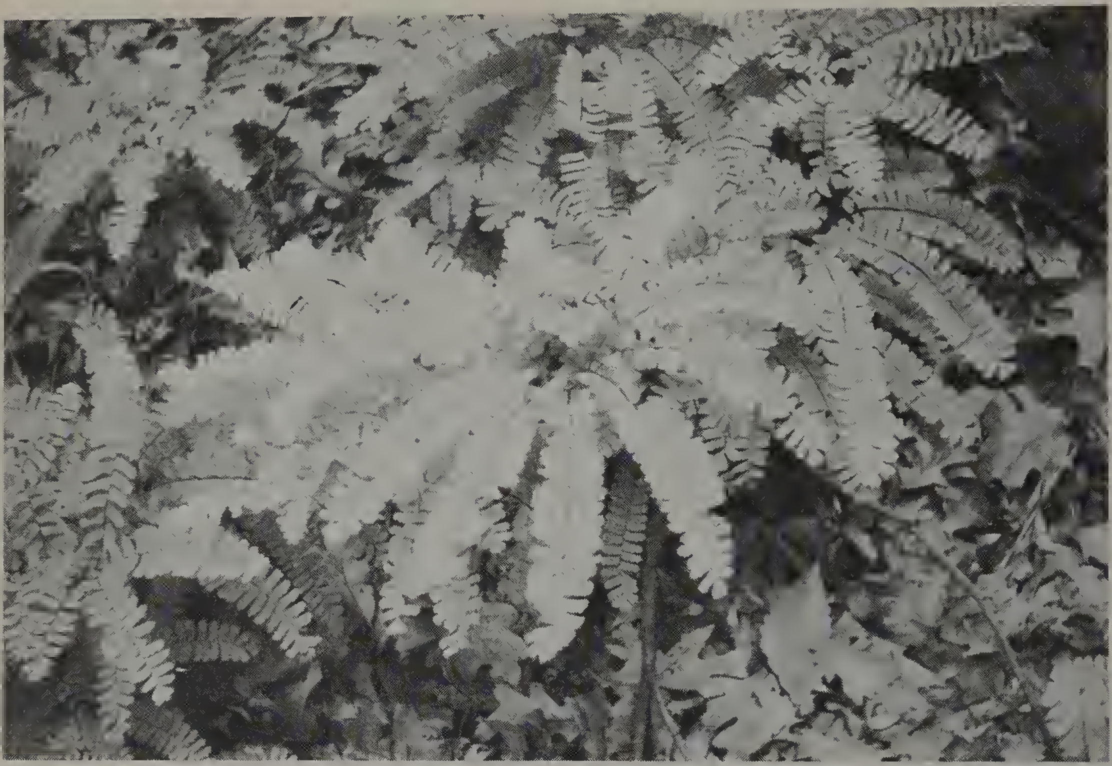
Fig. 6-14 Aspens, *Populus*, and gray birch, *Betula populifolia*, are dominant in this dry location.

and insect larvae are also present, especially in and under the rotting logs. Except in dry areas, salamanders may occasionally be found, taking refuge under stones and logs. The most common mammals of this stage are often white-footed mice and shrews, although the larger predators—foxes, raccoons, skunks, and weasels—play a part in such communities. Snakes, turtles, and lizards may also be quite common.

The Climax Stage

In those parts of the country where the oak-hickory community is the climax (p. 120), there may be only one tree stage in succession, the oaks and hickories growing up during the shrub stage. In such an event, the species of herbaceous plants which invade the developing climax community are those characteristic of the oak-hickory forest. For the most part these plants are the spring-flowering species, though mosses and ferns also become more common (Fig. 6-15).

If the climax type is to be composed of beech, hemlock, and maple, there may be several tree stages in which different



Allen H. Benton

Fig. 6-15 The ground in deciduous forests is often well covered with herbaceous plants such as the maidenhair fern, *Adiantum pedatum.*

tree species serve as dominants. Thus the aspens, gray birch, and cottonwood of dry areas may be superseded by red maple, white pine, and oaks, then by oaks and hickories, before the climax dominants make their appearance (Fig. 6-16). In mesic areas, paper birch and white pine may be followed by the climax forest, while in less perfectly drained areas red maple, willow, and cottonwood may be overtaken by such dominants as sycamore and sugar maple before the climax forest is established. There may be varied combinations of these dominants in intermediate stages, but as the climax type is finally approached, the communities become more and more similar; this is a process known as *convergence.*

The beech-hemlock-maple climax forest is mesic. It, too, has many herbs of the spring-flowering type, mosses, and ferns, often in more profusion than in the drier oak-hickory forest. Animals are similar to those in the earlier tree stages, but the vertebrates in particular are more abundant. This is partly because the climax tree stage shows stratification of habitats: the treetops are suitable to some species, lower branches to

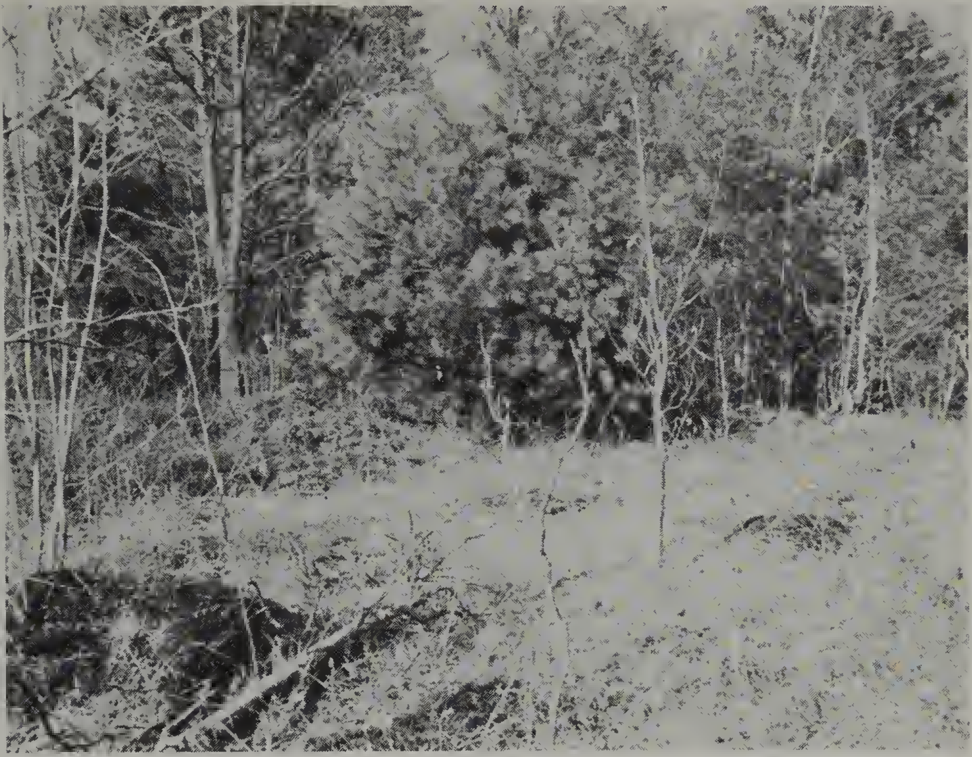


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Fig. 6-16 White pine and red maple, an intermediate stage before the climax forest is achieved.

others; the shrubbery provides habitat for still others; and some vertebrates live on and under the ground. The soil has now matured, and the species will not be replaced by others unless climatic or topographic change or some catastrophe alters the situation drastically. Shrubs that can tolerate shade, or cannot tolerate sun—such as witch hazel, maple-leaved viburnum, and flowering dogwood—may form an understory beneath the canopy of the dominants. But competition with invading species is for the most part over; now it is a matter of competition among existing species of the community.

As succession proceeds from the early pioneer community to the climax, there is a tendency for productivity to increase. There seems to be a lack of agréement among ecologists as to whether the optimum productivity occurs in the seral stages or in the climax stage. Whittaker (1953) states that productivity is greater in the late seral stages, while Olson (1963) found that in many ecosystems, productivity as measured by the accumulation of energy in organic matter will continue to show net increase until the climax is reached and even beyond.

Bliss and Cantlon (1957) found an increase in productivity from the pioneer to a second stage of development, and thereafter a decline. They measured productivity without including leaf litter, however, and there was deterioration of the site studied due to the effects of a meandering stream. Another way of regarding productivity and succession is to consider the ratio of productivity to the utilization of organic matter by all organisms of the community. During the seral stages, productivity will be greater than utilization, but when the climax is reached, productivity will equal utilization (Odum, 1963). Much more research involving measurements of productivity is needed in order to fully understand succession.

The description of succession from bare rock to forest climax is only one example of succession. The beginning might equally well have been a sand dune, flood plain, or sand bar; the climax perhaps prairie, coniferous forest, or tropical rain forest.* The manner in which the climax community reasserts itself is essentially the same everywhere. Even with widely differing origins, convergence is still the *tendency,* and a climax community the end point.

Speed of Succession

Since succession is a commonly observed phenomenon, either the process is lengthy, or new successional areas are constantly being created. We have seen that there are many agencies that may create new successional areas, which would lead us to suspect frequent origin of such sites. How long does it take, then, to restore these areas to a climax state? In the region around the Great Lakes there are still some boulders left by the receding glaciers of 10,000 years ago (Fig. 6-17). Some of the rocks are covered with lichens, the first stage of a primary succession, while other smaller rocks deposited at the same time by the glacier are well advanced in the seral stages and are now buried under the duff and in the soil of the forest floor. In the same region, the meadows of an abandoned farm may be repopulated with a climax forest within a hundred or two hundred years. On the prairies, an old wagon trail may

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* For examples of succession in the arctic tundra, see Bliss and Cantlon (1957); alpine tundra, Griggs (1956); taiga, Shelford and Olson (1935); deciduous forest, Smith (1928); grassland, Ellison (1960); desert, Wells (1961); and tropical rain forest, Kenoyer (1929).

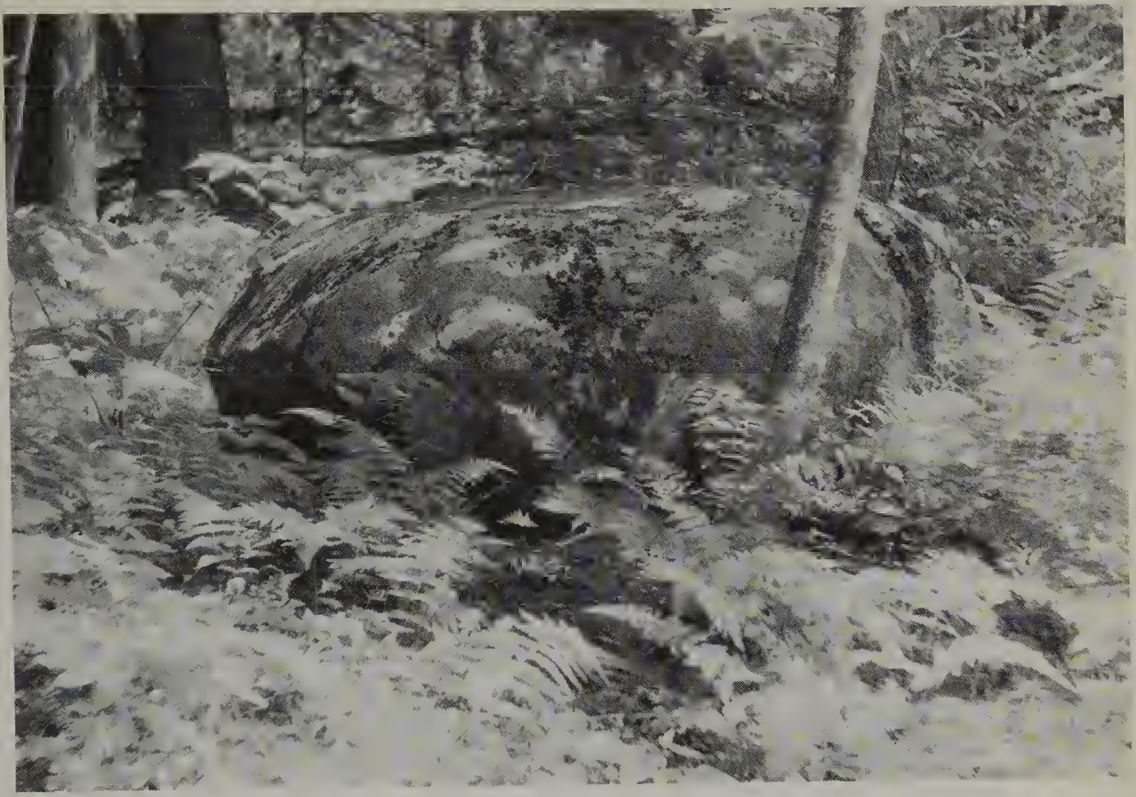

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Fig. 6-17 A glacial boulder in the midst of a hardwood forest, Petersham, Massachusetts. Only lichens have been able to colonize this boulder in the several thousand years since it was deposited here.

be revegetated with grasses in a far shorter time. In the desert, a rock may remain bare for a longer period than in a forested biome.

In many instances we do not know how long it will take for a sere to run its course. There are, however, several documented cases to give us some idea of the time that may be involved. Studies on lava flows in Mexico have indicated that lichens, algae, and mosses have invaded within 3 years after an eruption, flowering plants within 5 years, and trees and shrubs by 14 years (Eggler, 1959). However, the total process of succession on lava flows is lengthy, for after two centuries in climates best suited for soil formation, lava will be only slightly weathered, and thousands of years are probably required for production of soil. Various landslides in New Hampshire known to be from 3 to 72 years old were studied by Flaccus (1959). The surfaces of bare rocks, bared till, and slide talus remained largely uncovered by vegetation after 72 years. Mosses and lichens did appear on one slide 19 years old. In the residual forest soil remaining or collected between rocks, herbs, shrubs, and trees became established in 9 years. After 72 years the herb layer was virtually similar to the surrounding forest, and the tree species composition was approaching the climax. In Glacier Bay, Alaska, early explorers noted that a glacier started receding about 1800. Cooper (1939), studying the area in 1935, found a forest approaching climax composition on the site, with the oldest trees 121 years old. Thus, a rapid succession has occurred in this case with the establishment of climax tree seedlings soon after the recession of the glacier. Martin (1959) used the age of trees and stumps as calculated by growth rings, historical data, his own and other workers' observations on various stages of succession in the area, and the known maximum length of life of trees in estimating the length of the sere in Algonquin Park, Ontario. He concluded that there the climax stage could be reached in 1,100 years, barring interruptions.

Climate, the extent of disturbance from the climax, and other factors may alter the time it takes for succession to be completed; but in most cases succession is a relatively short-time phenomenon. It would seem that the frequency of its occurrence is in large part due to new areas undergoing a change which destroys the climax community. In an over-all view, we see that any community, including a climax, is stable in only a limited sense. Actually, there are always within it some areas that are being destroyed and some that are undergoing an orderly growth back to the climax community.

To summarize, succession involves at least four basic concepts:

1. There is a dynamic shifting of the species composition of the community.

2. The species change is an orderly one, so that barring further interruptions, it may be predicted what type of community will follow an existing one.

3. The sequence of changes of the community types is directional, with each succeeding community type becoming more like the climax type, at least in physical characteristics.

4. The ultimate community type is the climax community.

SPECIAL CONSIDERATIONS

At this point, it might be well to consider some special situations, difficulties, and differences of opinion among ecologists concerning succession and climax. Among the topics we will discuss are microsuccession, some possible exceptions to the general phenomenon of succession, the role of interruptions, other special situations in succession, and the problem of defining the climax.

Microsuccession

It was mentioned earlier in this chapter that within communities there are small variations, and that a miniature succession occurs here. This kind of microcommunity succession may be found, for example, in dead trees, animal droppings, carcasses, and plant galls. Such situations provide microhabitats where communities of plants and animals live, succeed each other, and finally come to an end by the destruction of the habitat as it becomes part of the larger community.

Galls offer an example of a simplified animal succession in a microhabitat which may help in understanding this phenomenon. In studying the ecology of the goldenrod ball gallfly *Eurosta solidaginis*, Uhler (1951) discovered that the gall formed by this fly served as a home for several insects, some of which prepared the way for others, and in so doing, made the habitat unsuitable for further tenancy by their own species.

The goldenrod ball gall (Fig. 6-18) is an abnormal growth of plant tissue found in the stems of goldenrod (*Solidago* sp.). It is formed after the fly inserts an egg into the growing tip of the young goldenrod, and the young larva hatching from the egg eats its way to the meristematic tissue. This tissue, probably due to some stimulation from a substance in the saliva or feces of the larva, forms a growth around the larva which may reach dimensions of about 20 by 25 millimeters. Thus the animal has caused a change in its environment, in this case the interior of the plant. The larva eventually eats out the center of the gall, to form a chamber in which it will overwinter. In the following spring, it will pupate and emerge as an adult, but during the adverse conditions of winter the plant gall has served as food and protection and has probably produced a stabilizing effect on humidity and temperature. After pupa-

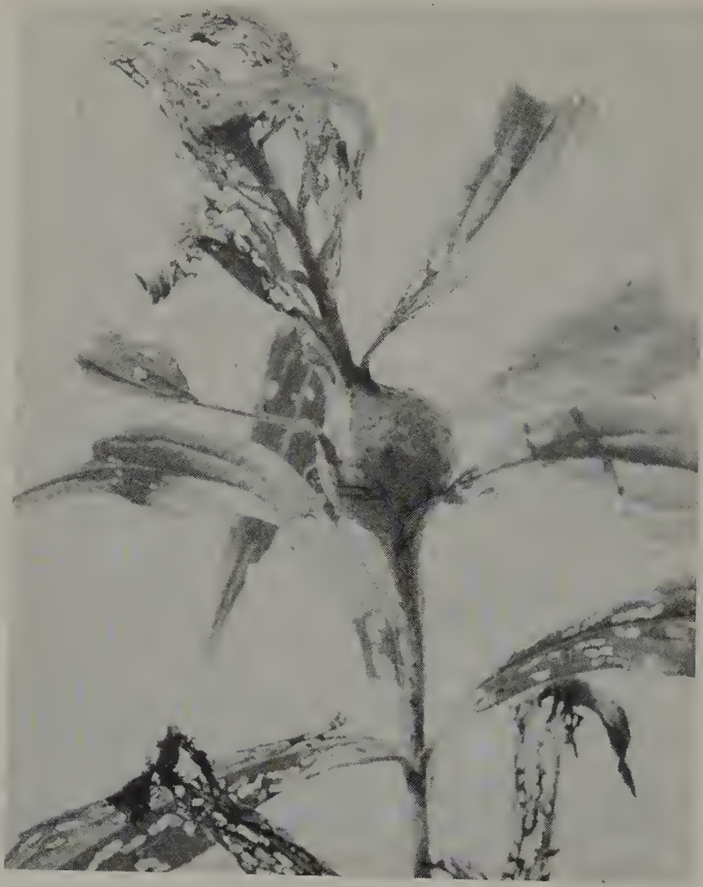

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Fig. 6-18 A goldenrod ball gall caused by the gallfly, *Eurosta solidaginis.*

tion of about two months, the adults emerge to start the life cycle over again, but the old gall is no longer suitable and is not used again by the fly. It has been made undesirable for further use by this species, at least in part by its own activities.

Sometimes, to the confusion of students of galls, the fly which caused the gall does not emerge from it, but some other insect does. The emerging insect is a parasite or predator on the larval fly and so is part of the first community in this succession. Two species of gall wasps, both of the genus *Eurytoma,* parasitize and finally eat their host, the larval gallfly. In the spring of the host's intended pupation and emergence, these parasites begin their new life cycle. In spring also, while the gallfly pupa is still within the gall, another insect—a beetle larva of the genus *Isohydnocerca*—may enter the gall and devour the fly. There may also be gall gnats of the family Cecidomyidae living in the gall, feeding on the plant tissue.

These little gnats contribute still more to the community with their own parasites. In the meantime another beetle, of the genus *Mordellisterna*, finds this developing community attractive and eats its way into the gall, feeding on its tissues and occasionally upon the host.

The next major stage of this succession begins as these inhabitants leave the hollow gall, no longer suitable for them. Now a wasp, *Ancistrocercus tigris*, uses the empty sphere to lay eggs and store paralyzed caterpillars on which its larvae will feed. These wasp larvae are parasitized by several other insects, which may therefore be found in the gall during its second summer. Beetles, thrips, and ants may use the empty galls as a home, some perhaps only temporarily. Finally this second major stage ends after the second winter, as the dead goldenrod falls to the ground.

While the gall lies on the earth, it may be used briefly by invertebrates before they, along with bacteria, bring about the ultimate destruction of its tissue in this third and final stage. The organic remains of the plant, the fecal material from the many animals which have lived in it, and perhaps the remains of parasitized insects will now be added to the soil. Thus the successional pattern in this microhabitat has ended. Each succeeding community has utilized the gall after preparation of suitable conditions by the members of the former community. The end point, as is true of most microsuccessions, is the community type in which the microhabitat existed, in this case probably a meadow.

The processes of change which bring about succession are fundamentally the same, whether they occur in microhabitats such as the one just described, or in the larger habitats in which these smaller ones exist.

Retrogressive Succession

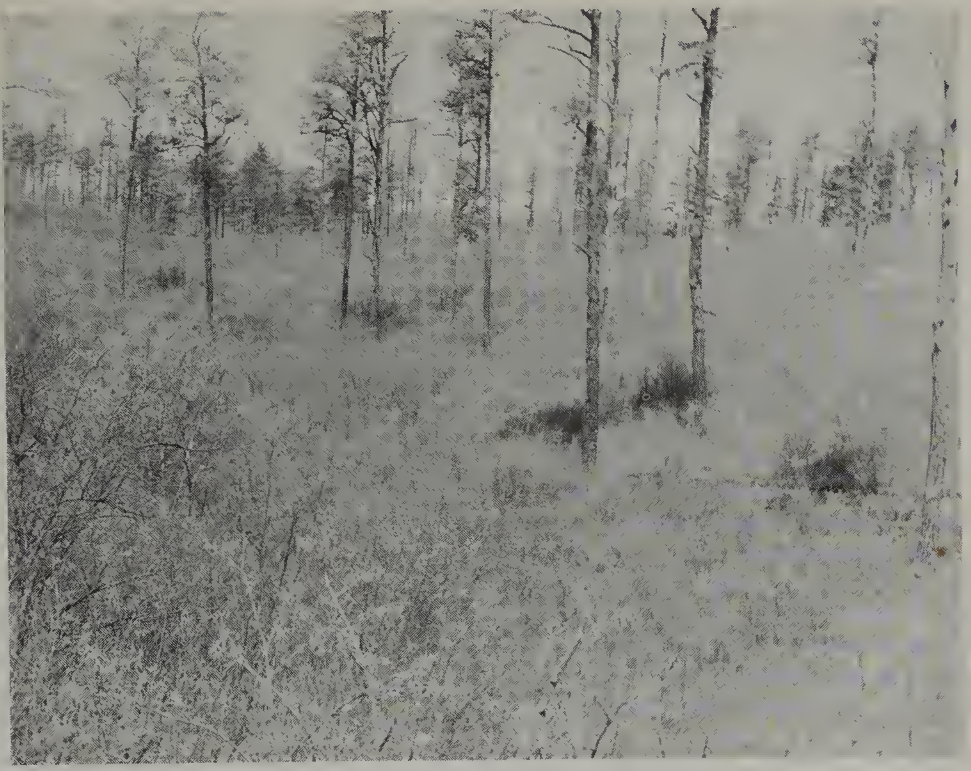
So far we have assumed that the sere leads to a "higher" type of community with more mesic conditions. On occasion, however, a situation will occur in which a community deteriorates, and a new stable community develops. Some ecologists (Tansley, 1935) have called this *retrogressive succession* and point out that a true development (sere) to a new community occurs. Other ecologists insist that the new community is merely established at the expense of the deterioration of the site and tend to overlook the development to the new community as a sere.

An example of the phenomenon in Alaska is described by Lawrence (1958), where on gentle slopes or flat terrain after a glacier recedes a typical succession proceeds through herb and shrub stages to a spruce forest. Under the spruce there are found typical forest mosses and a second generation of smaller trees. Then rather suddenly there is an invasion of sphagnum mosses, which are capable of holding large quantities of water. The spruce trees die as their roots are deprived of air. Eventually an open forest of a few scattered trees of species which can tolerate the wet situation (mountain hemlock, Pacific coast pine) are the only survivors. This condition is apparently maintained for thousands of years, while on nearby hilly and drier terrain, a forest with a closed canopy remains.

Another example of this process may be found in areas that have been burned frequently. One such area may be observed between Albany and Schenectady in eastern New York. Here an area of sandy soil covers a wide belt some twenty miles long and five or six miles wide. Much of this land was once covered with a climax forest of white pine. With increased population of the region, the trees were cut, and parts of the sandy soil were farmed for a time. Fires occurred frequently, burning what little humus was present, and the whole area became a sandy plain. White pine could not tolerate the fires, but another pine which occurs in this region, the pitch pine, could withstand both fires and the poor soil. Today the pitch pines grow scattered about as in a savanna, and the main vegetation beneath them is a dense growth of shrubs, including bear oak, shrub oak, dwarf cherries, and staghorn and smooth sumac (Fig. 6-19). Most of these shrubs occur in small numbers elsewhere in this region. Here the bushes and dwarfed trees are dominant, or at least codominant with the pitch pine, and they form a community distinct from any in the nearby region. Indeed, no seral stage of normal succession in this region resembles this vegetational type. Yet if the fires and other results of human activity were ended, the area's normal climax would eventually be reestablished. Such an area is referred to as a *disclimax*.

Delays in Succession

In the earlier discussion of primary succession, a sere was described in which an herbaceous community was invaded by



Allen H. Benton

Fig. 6-19 A pitch-pine–shrub-oak community maintained in a disclimax condition by human activities.

shrubs and sapling trees and then the shrub community was displaced by a forest. Sometimes this process may be so slow that succession appears arrested. Thus Buss (1956), in a study of fields in Wisconsin uncultivated for 22 to 35 years, noted a relative lack of woody-species invasion. Often the shrubs are thought of as providing shade, thereby permitting shade-requiring tree seedlings to invade. There are, however, instances in which shrubs may delay the tree stage. How long the delay may be would vary with circumstances, but Niering and Egler (1955) found one community of nannyberry (*Viburnum lentago*) in which these shrubs were at least 25 years old and still formed a dense closed thicket with little evidence of invasion by trees. Aller (1956) describes a shrub community in Oregon dominated by vine maple (*Acer circinatum*) and Sitka alder (*Alnus sinuata*) at least 100 years old. The stand is so dense that conifer seedlings cannot become established. This shrub community is apparently maintaining itself, and there is no evidence that fire is involved in its stability.

Complexity of Successional Patterns

Even where situations may seem simpler, as in the partial disturbance of a climax forest, the pattern of succession may be complicated. Godman and Krefting (1960) found that when yellow birch trees were lumbered, the seedlings of remaining birch trees found it difficult to become established because of competition from rapidly invading blackberry and raspberry bushes. The invasion of shrubs also caused the rapid loss of favorable seedbed conditions created during lumbering operations. Finally, sprouting by red maple trees was a further complication because of the rapid initial growth of its sprouts compared to the slow growth of the birch seedlings.

Sprouting is a growth characteristic of great significance in forest succession. Chestnut trees are still sending up sprouts, even though the stumps of the former mature trees have mostly rotted away. If some species sprout easily while others do not, a community may easily have its composition changed after a disturbance. Much of the New England oak-hickory forest is a sprout forest, as can easily be detected by observing the numerous multiple-stemmed trees. But one might well ask what species may have been eliminated or reduced from these communities through inability to sprout after fire or lumbering.

Interruptions

In considering the sequence of communities in a sere, we might assume a lack of interruption after the initial one. However, this assumption is probably unrealistic, especially where the length of the sere is several centuries. Of all the interruptions that may happen to a sere, fire is one of the most likely to occur, judging by its frequency in the past. Fire has been much more common in "nature" than most people realize, and when man attempts to control it, he may be working against his own interest. For example, Cooper (1960) points out that the southwestern open pine savannas are a result of centuries of fires. With fire control and exclusion of grazing livestock, a closed forest canopy is developing and the grasses are disappearing. When a fire has occurred, the direction in which succession will proceed may well depend on the sprouting habits of the trees, shrubs, and vines present, as in southern pine forests (Hodgkins, 1958). Once disturbance of a forest by fire has occurred, the invading herbs and shrubs may provide fuel for subsequent fires, and eventually the forest may be eliminated, as in certain areas of California (Wells, 1962). When the vegetation is so drastically altered, it is only logical to assume that the animal component of the community is also altered. Thus destruction of ground cover and invasion by annual seed-producing plants may initially favor certain seed-eating small mammals but be disadvantageous to those requiring a thick layer of mulch (Cook, 1959). In some cases, small mammal populations in recently burned areas may increase to two or three times the density found in an adjacent climax forest (Gashwiler, 1959).

Absence of Succession

Some ecologists have found evidence that in some areas of the desert, succession may not occur at all. When a community is disturbed, the species which invade merely become more abundant instead of being replaced by new species (Muller, 1940). Shreve (1942) felt that the lack of successsional phenomena in desert communities may be explained by the lack of accumulation of leaves and twigs, which are blown away. Plants are thus less able to alter the environment. However, a study by Wells (1961) of succession in an abandoned desert mining town illustrates that succession does occur at least in some desert areas and indicates that a new look should be taken at desert succession.

Climax Theories

The concept of succession involves the idea of a gradual change of communities toward a stable community, the climax. But how does one know when the climax is reached? How does one recognize a climax community? In what ways are climax communities different from successional communities? How one answers these questions depends in large degree on one's conception of the discreteness of climax communities, on what is considered to be the control or controls of climax stability, and on how rigidly one defines climax stability.

Many workers have noted that a climax community is not perfectly stable; it is merely more stable than a seral community. Olson (1963) pointed out that accumulation of energy of an ecosystem increases until the climax is reached and then oscillates around an average. Evers (1955) observed a shifting equilibrium between forest and prairie in Illinois, and Buell and Martin (1961) noted a similar phenomenon in Minnesota between two forest climaxes. In these cases a shifting of climate caused periodic fluctuations in climax communities. As we shall see, there may be other factors which could cause minor instability of the plant components of climax communities. Not the least of these other factors are the animals of the climax, whose populations may fluctuate widely. Thus, stability of a climax community is only relative to that of a seral community.

Generally, in a forest climax the many young saplings will be the same species as the mature trees. There will be a tendency toward regularity of species composition on sites having similar environmental conditions. As mentioned earlier, productivity will have reached a stable state. However, a major consideration in the definition of climax is what factor or factors determine the stability and composition of the climax. Differences of opinion in this matter are the basis of several theories regarding the climax.

The Monoclimax

An early concept of climax was developed by Clements (1936). According to this theory, there is only one true climax in a climatic region. There are usually several such climatic regions within a biome, each region having its distinct climax. Each climax is, however, the end point of succession over a large geographic area. Given time, all communities in a climatic area will become alike (convergence) as conditions become mesic. Certain species will be dominants and thereby control the species composition of the climax. The vegetation will react upon the soil, producing uniformity of soil throughout the climatic region despite any differences in original parental rock or soil conditions. If various situations prevent the attainment of mesic conditions and complete convergence to the climax, these are considered unusually long delays in succession. Various terms such as subclimax, disclimax, postclimax, and preclimax are used to describe the deviations from the climatically stabilized climax.

Polyclimax

Another viewpoint or theory regarding climax holds that if a community becomes stabilized for a relatively long period of time, it may be considered a climax, even though convergence to mesic conditions is not complete. According to this theory, climate is only one of several factors, any of which may have a controlling influence on the structure and stability of the climax. This allows many climaxes in a climatic region and is therefore called the *polyclimax* theory. Thus a stable community on most favorable soils (mesic conditions) would be the climatic climax; on less favorable soils, an edaphic climax; on rugged topography (which would produce local climates), a physiographic climax; where there is continual disturbance by fire, grazing, or other causes, a disclimax; and so forth. The difference between this theory and the monoclimax theory is largely a matter of emphasis on which factor is responsible for stability of a climax. In each case there are discrete climaxes, hence only a limited number of them.

Climax Pattern

Some ecologists have noted the continual variation of communities and have been unable to accept the grouping of climax communities into a relatively few discrete types as provided by the two theories discussed above. One alternative theory is proposed by Whittaker (1953), who has studied such complex areas as the Smoky Mountains of the Appalachians and the Siskiyou Mountains of Oregon and California. He sees the climax community as varying continuously in space along environmental gradients, and to some extent varying also with time. Thus he is not concerned with naming a climax as climatic, edaphic, or physiographic or deciding whether a stable community is a climatic climax, subclimax, preclimax, or postclimax. Probably several environmental and other factors may have been simultaneously involved in producing a variation in a climax community composition. Furthermore, since each species within a community has slightly different ecological requirements and geographic distribution, one does not expect to find identical species composition from one spot to another. Accordingly, abrupt changes in species composition of climax communities occur only where there are abrupt changes in environmental gradients. Changes of the climax composition may also occur with time, as climate oscillates slightly, genetic changes occur, ranges of species change, and interruptions such as fire, insect attack, and windthrow provide opportunities for invasion of competing species. Regarding soil formation, this theory holds that the climax type is not independent of parent soil material, but that soil and environment are related in a complex fashion.

Many factors are involved in shaping the composition of a community. Whittaker (1953) lists nine major factors: genetic structure of each species, climate, site, soil, activity of animals, fire, wind, availability of plant and animal species, and chances of dispersal. Thus, according to this theory, climax communities are patterns of populations varying according to the total environment. There is thus no discrete number of climax communities and no one factor that determines the structure and stability of a climax community.

Climax as Vegetation

Another position regarding climax is represented by the views of Egler (1951, 1964). He does not use the word climax. He feels that the monoclimax and polyclimax theories are scientifically unsound, that they include inconsistencies, that they indulge in an overabundance of terminology, and that they stress the study of assumed virgin states and stable conditions, whereas in actuality most communities show the effects of past disturbance, not the least of which are man-made. Moreover, after describing so many stable or climax communities, one can say that "climaxes" in a broad sense are nothing more than the totality of vegetation itself. Egler thus favors the study of vegetation as it is, with careful observations to explain and interpret past, present, and future conditions of particular communities. He also feels that the succession-to-climax approach to ecology is too simple and favors, instead, approaches recognizing both the "individualistic concept," whereby species act independently of each other, and the ecosystem concept, whereby bio-communities and the environment are integrated into larger wholes. In the latter instance, problems dealing with energy relationships which are amenable to quantitative techniques and statistical analysis are fruitful fields of inquiry.

One may elect to follow one of these or other viewpoints or theories of climax and vegetation, or possibly to combine certain aspects of all or some of them. As we have seen in this chapter, succession is a frequently observed phenomenon in nature, although often it is of the secondary type, and sometimes is quite complicated by centuries of interruptions by man and other forces of nature. An end point of succession is possible, however, and this end point, or climax, is in itself not completely stable. Although climate theoretically plays the controlling role in climax determination, in actuality, various other factors are often involved. Climax communities, like other communities, are aggregations of organisms which are more than the sum of their parts; they form an integrated whole. However, the boundaries of climax communities are usually not discrete, because of environmental gradients and other factors. The ideal way to study communities is through the ecosystem approach, the consideration of the organisms and their environment in all their relationships. One aspect of this total picture can be observed by considering the way in which relatively stable communities evolve, that is, through a study of succession.

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chapter 7

Succession in aquatic communities

In the discussion of terrestrial succession, it was mentioned that aquatic areas also undergo succession, and that both processes were basically similar. Lakes, ponds, bogs, swamps, and streams all possess a variety of communities of plants and animals which are unlike any found on land. These communities are similar to the terrestrial ones, however, in that they are also dynamic and change in an orderly fashion toward the climax community. The factors bringing about the changes are somewhat different from those in terrestrial situations, and in many instances the physical elements are more important in accomplishing the succession. Perhaps because of this fact, aquatic developments are sometimes described as "evolution" of aquatic situations, even though a true succession does occur.

Aquatic Environments

There are two major kinds of aquatic successions. One involves still bodies of water (*lentic* environments) such as

One cannot step into the same river twice.

Heraclitus

lakes, ponds, bogs, and swamps. The other type includes brooks, creeks, rivers, or other moving waters (*lotic* environments). Lentic environments evolve by means of a combination of physical and biotic forces. These forces operate to fill in the basin of the body of water, or drain it, or both. Thus lakes become ponds, ponds become bogs, and these finally evolve into solid ground. As such changes occur, the communities in them undergo succession and help to bring about the changes.

Lotic environments, on the other hand, evolve for the most part as a result of physical forces alone, the direction of evolution being from brook to stream, stream to river, or more exactly from fast to slow stream. The succession goes from swift- to slow-water communities, the latter in some respects similar to pond or lake communities. The climax of the lotic sere is therefore different from that of the lentic, which culminates in a terrestrial climax community.

As in terrestrial situations, one is confronted with the problem of origin and rate of change of the aquatic environments undergoing succession. Are lakes and ponds being created continually, or does lentic succession proceed slowly? The abundant examples of bodies of water themselves do not give us the answer, but a study of geology and succession does. Lentic environments evolve slowly, and only occasionally are new lakes or ponds formed.

THE FORMATION OF LAKES AND PONDS

There are many ways in which depressions or basins may be created where water may collect to form a lake or a pond. Hutchinson (1957) lists 76 different processes by which lakes may be formed, although these are grouped into only 11 major categories. Some of the common types will be described here.

Tectonic Lakes

Lakes formed in basins created by movements of the earth's crust are called tectonic lakes. Occasionally, as the earth's crust shifts, a fissure may form or a narrow strip of the land may sink. This is a process known as faulting. Such fissures or sinks may fill with water and form lakes known as rift lakes. As one might expect, these lakes are long and narrow. They may also be deep; the deepest lakes known are of this type, e.g., Lake Baikal, Russia, 4,992 feet; Lake Tanganyika, Africa, 4,707 feet. The basin of Lake Tahoe in California-Nevada is a down-faulted trough deepened by a lava-flow dam at one end (Fig. 7-2). Reelfoot Lake in Tennessee was produced as a result of an earthquake in 1811.

Lakes may also be formed by elevation of land, cutting off arms of the sea. Lake Ontario, as stated on page 165, is an example of this type of lake. Lake Okeechobee in Florida was formed from the gradual uplift of land from the sea, exposing a preformed natural basin.

Volcanic Lakes

Another type of lake is produced by volcanic activity, and such bodies of water are known as crater lakes (Fig. 7-1). Once a volcano becomes extinct, its hollow interior may fill with water. Frequently these lakes, like rift lakes, may be very deep, although they are circular in outline. Crater Lake in Oregon—in part formed by volcanic activity and in part by the shifting of the earth's surface—is 2,000 feet deep. Mono

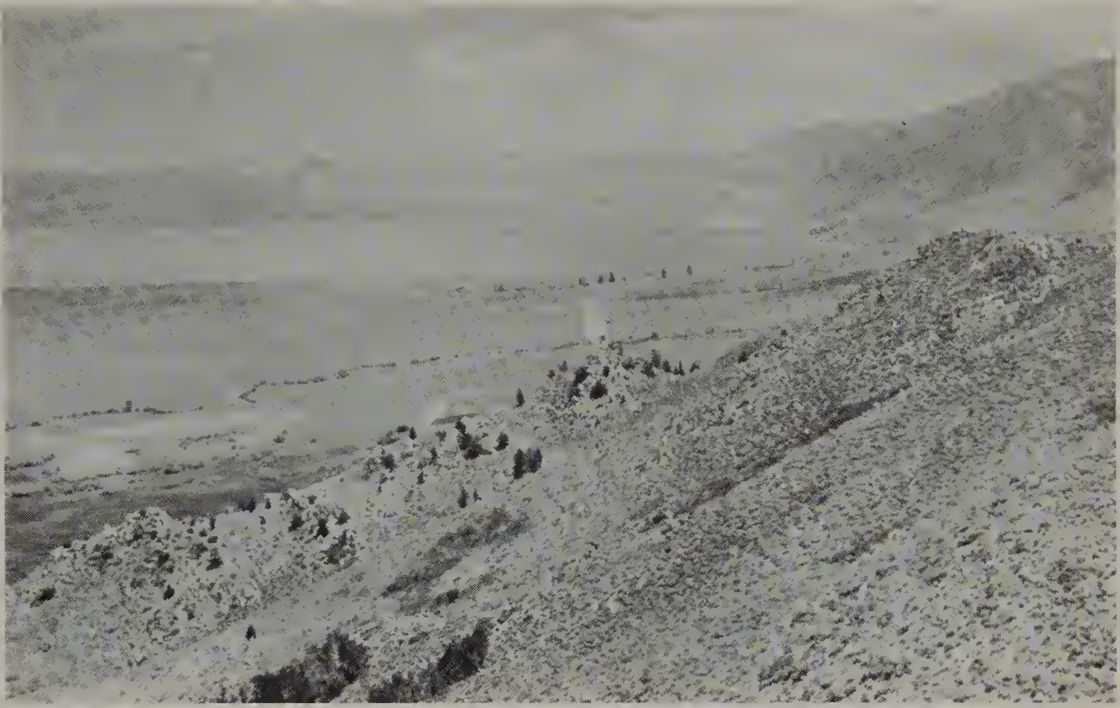

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Fig. 7-1 Mono Lake, California, a lake formed in the crater of an extinct volcano.

Lake, California, is in a basin produced by volcanic activity. Within it is an island on which there are other much smaller volcanic lakes.

Glacial Lakes

Glacial action has provided the earth with many of its lakes. As glaciers move over land, there is a tendency for them to gouge out previously existing valleys, for the ice is plastic and fills up the valleys, forming a higher and consequently heavier cover here than on the higher areas. The result is that in these valleys deep lakes with steep sides may form when the glacier melts. Many of the lakes of northeastern North America owe their formation to such glacial action. A striking example of lake basins deepened by glaciers is that of the Finger Lakes of central New York. If a glacier stops advancing at the end of a valley, the rocks and soil incorporated in it (glacial drift) may be dropped at the point where it stopped, forming a terminal moraine. This moraine may act as a dam across the end of the valley, forming a lake or increasing the depth of a pre-existing lake.

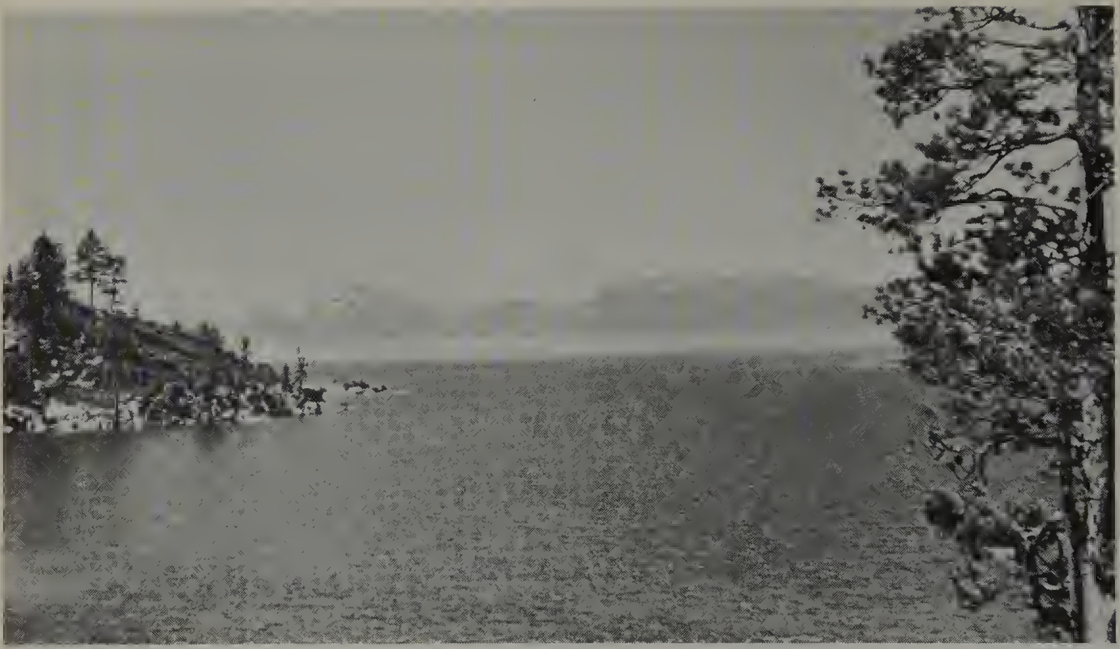

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Fig. 7-2 Lake Tahoe, on the California-Nevada border. This lake was created by tectonic activity plus a lava flow dam.

When glaciers start melting, large pieces of ice may be left behind, and their weight may form a depression which will eventually become a small lake or pond. Ponds and small lakes of such an origin are generally distributed over recently glaciated regions.

Lakes Formed by Other Processes

Lakes may also form under a variety of other conditions. Occasionally, they have their origins in the dissolution of rocks under the surface. An example of this type of lake is Deep Lake in Florida, which formed as the result of the dissolution of limestone under the ground. Landslides may block off valleys, forming dams behind which ponds or lakes may develop. Clear Lake in California was formed as the result of a lava flow which blocked one outlet of its basin, followed by a large landslide across the other exit. More frequently encountered are ox-bow lakes, created by meandering streams cutting S-shaped beds in a valley floor. The curves may become so extreme that the stream comes together at its bends, and a whole arm of the stream may be cut off, eventually to form a crescent-shaped lake alongside the stream. Other

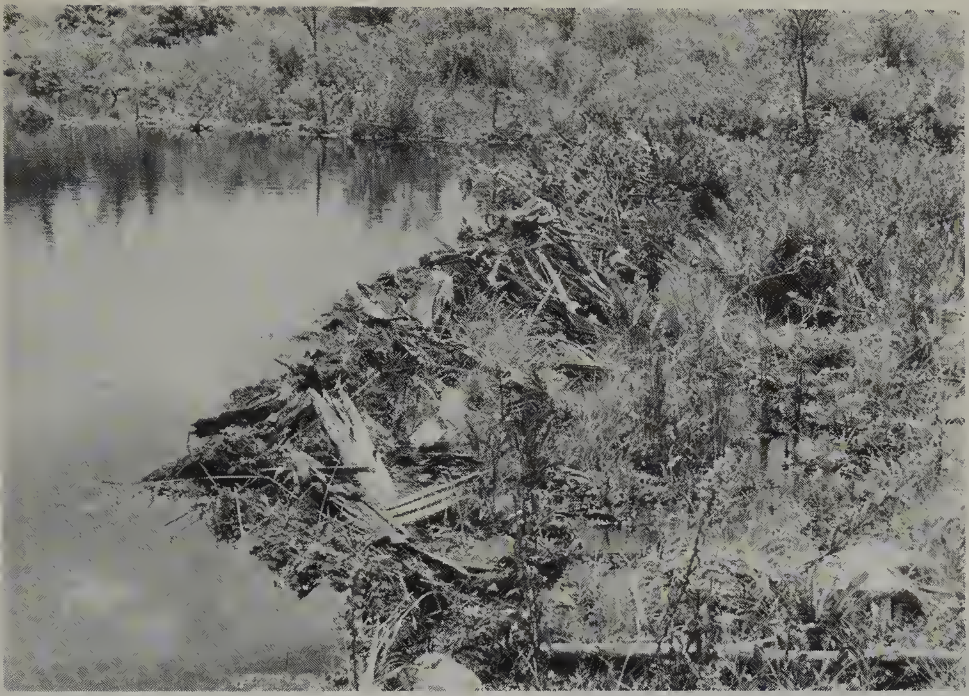

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Fig. 7-3 A beaver dam in western Maryland at an altitude of about 3,000 feet. Numerous dams in the region have created an extensive boggy area, as well as small ponds.

lakes may be formed at sites where rivers empty into the sea. Wave action or siltation may dam the river's exit and form either a fresh-water or brackish lake.

The activity of animals is another cause of pond formation. Beaver dams across small streams may produce a large though shallow pond (Fig. 7-3), while wallows of animals like the buffalo may form temporary ponds. Man's activity accounts for many bodies of water, not only by intent (the large irrigation and power dams, reservoirs, and farm ponds), but also by chance (bodies such as those which result from quarrying and mining).

CLASSIFICATION OF LAKES

Biologists who study inland waters are known as limnologists, and the science of limnology may be considered a part of the broader field of ecology. Limnologists have classified lakes into three categories according to the amount of plant and animal life which the waters sustain.

Oligotrophic Lakes

Lakes which do not produce abundant organisms in relation to their volume and which always possess abundant oxygen in their lower regions are called *oligotrophic* (little-producing) lakes (Fig. 7-4). They are usually deep lakes. Like other deep lakes, during the summer they often have at the bottom a region of cold water (the *hypolimnion*) which is of greater volume than that of the upper region of warm water (the *epilimnion*). The hypolimnion in oligotrophic lakes contains considerable oxygen at all times. Separating the epilimnion and hypolimnion is the thermocline (Fig. 7-7), a layer in which the temperature of the water falls very rapidly with increasing depth. By definition, the decrease in

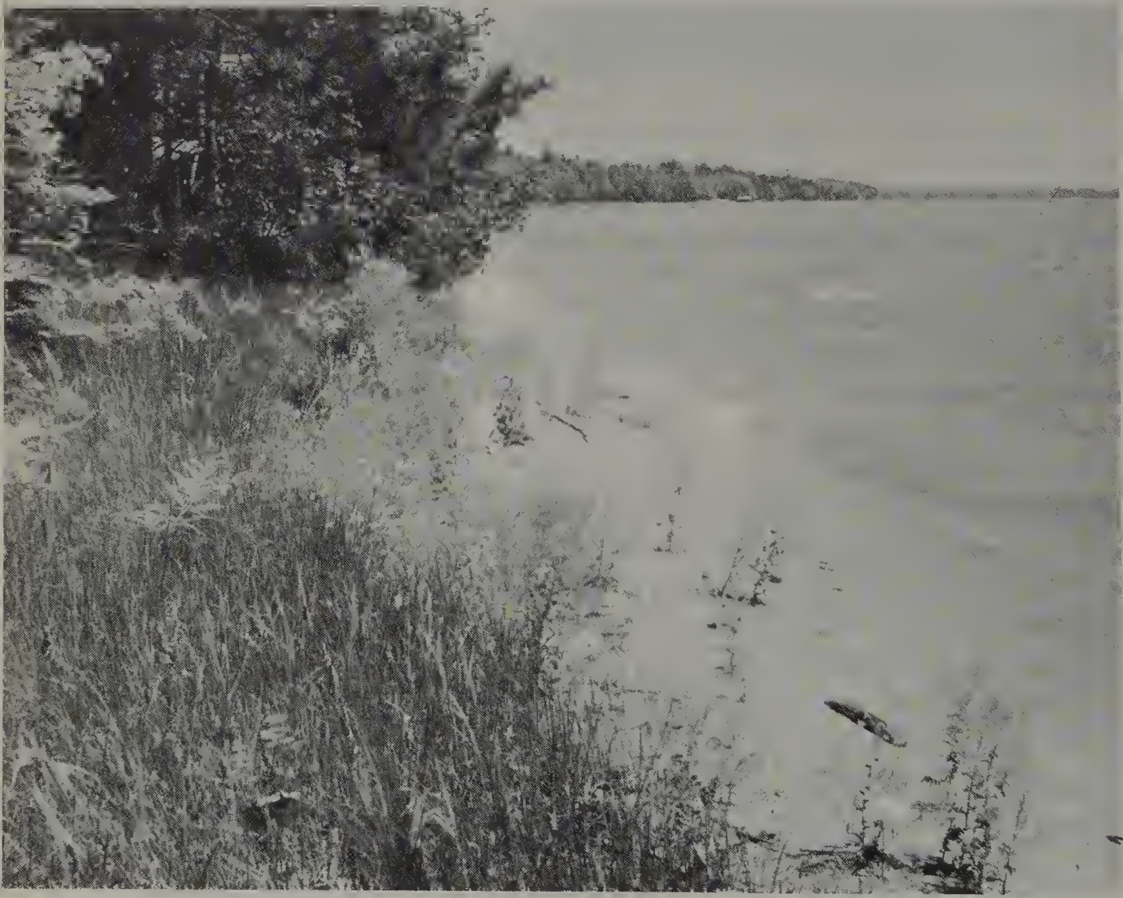

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Fig. 7-4 An oligotrophic (little-producing) lake. These lakes are usually deep, with a region of cold water near the bottom and little plant life. Higgins Lake, Michigan.

temperature must be at least 1° Centigrade per meter of increase in depth, or 0.548° Fahrenheit per foot.

A relatively shallow (though still "deep") lake may be oligotrophic because there are so few organisms produced that little oxygen is expended in their decay on the bottom, while a deeper lake may be more productive of organisms but remain oligotrophic because the hypolimnion is so large that there is ample oxygen to decay the organic matter without undue depletion of the oxygen (Macan and Worthington, 1951).

There may be other factors involved in creating oligotrophic conditions, such as the shape of the lake basin, direction of the prevailing winds with respect to the orientation of the lake, and amount and nature of chemicals and organic materials washed into the lake. However, the classification is still based on productivity as indicated by the resulting condition: oxygen is never depleted in the hypolimnion.

Eutrophic Lakes

Good-producing, or *eutrophic*, lakes (Fig. 7-5) sustain a rich plant and animal life. Such lakes are usually shallow and have a hypolimnion smaller than the epilimnion. During the summer all the oxygen in the hypolimnion is used up by oxidation of dead organic matter on the bottom. Organic materials are abundant both in the water and on the bottom.

Dystrophic Lakes

The third class of lakes is given the name *dystrophic*, or bad-producing (Fig. 7-6). Such lakes may support plants and animals of certain types, but their growth is slow. Dissolved organic matter is high and imparts a brown stain to the water. The brown color severely limits the depth to which light may penetrate and thus also limits productivity. Decomposition of some of the abundant organic material may completely use up the oxygen during some seasons and thereby affect the productivity of such lakes. Much of this organic matter is not produced in the lake itself but in surrounding areas (Ruttner, 1963). There is so much organic substance that it cannot all decompose and instead accumulates as peat on the bottom. Lack of calcium, characteristic of dystrophic lakes, may also be involved in the incomplete decomposition (Macan and Worthington, 1951).

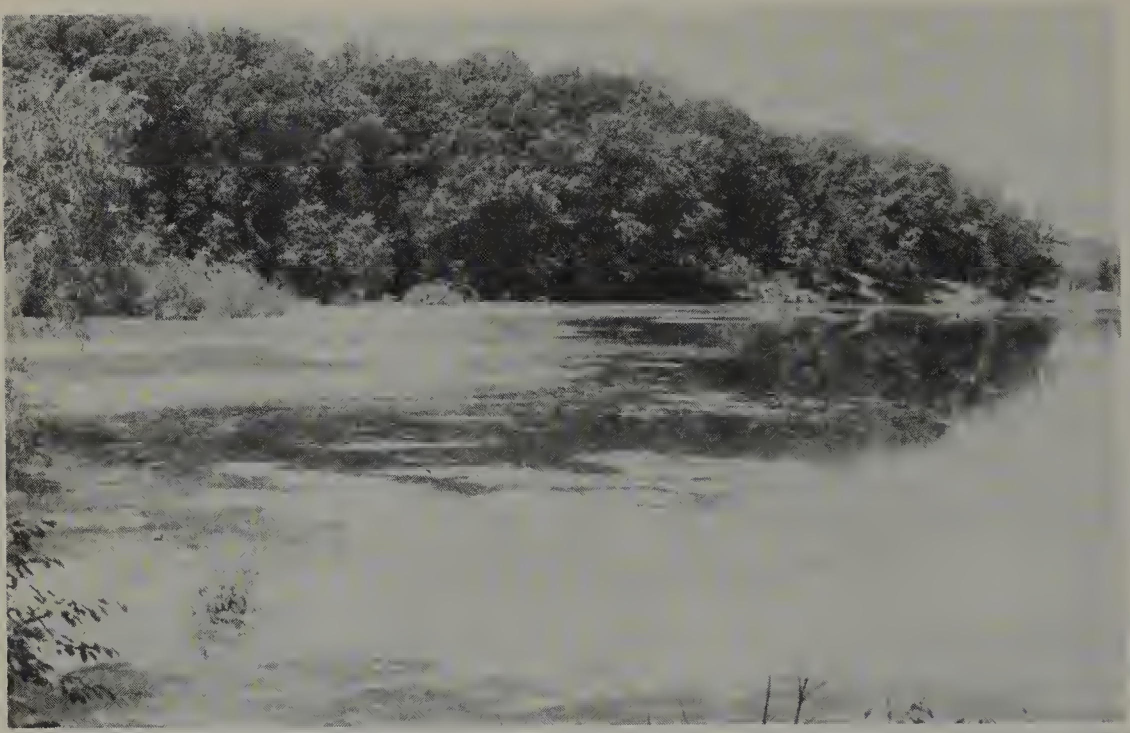

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Fig. 7-5 A eutrophic (good-producing) lake, with rich plant and animal life. Algae and duckweed float on the surface. Beaver Dam Lake, Macoupin County, Ill.

SUCCESSION IN LAKES

The line of evolution or succession of lakes may begin with oligotrophic lakes. These are the deepest type of lakes, so that ordinarily more time is required to change them to dry land. All lentic environments may become dry by two major processes. They may fill up with materials washed into the basin and with the remains of dead organisms which once lived in the lake, or the outlet may cut down its stream bed so that eventually it becomes level with the bottom of the lake. Some oligotrophic lakes are so deep that they do not appear to be changing, yet surely some sediment must wash into the lake through tributary streams and some organic matter must be deposited on the lake bottoms. From data secured by means of cores on the bottom of one lake in England, Macan and Worthington (1951) indicate that only 30 feet of sediment have accumulated in the last 11,000 years. In a study of lakes in Colorado, Pennak (1963) found that the rates of filling varied from 0.19 millimeters to 0.53 millimeters

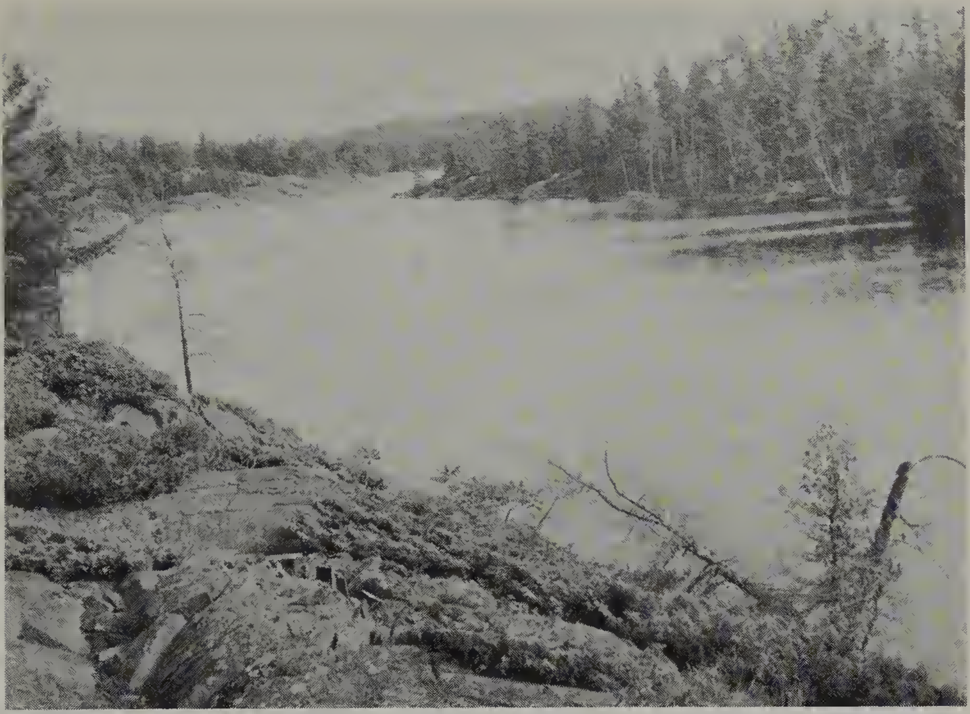

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Fig. 7-6 A dystrophic (bad-producing) lake, with water stained brown by undecayed organic matter. On an island in Lake Huron, Canada.

a year in different lakes. Longwell and Flint (1962) estimate that Lake Erie may be filling at the rate of three inches in a hundred years, while Niagara Falls is receding at the rate of four feet a year. The lake is already 15,000 years old, and we may expect it to be filled and drained in 27,000 more years. There may be considerable variation in the rate of filling even in the same lake, but filling and draining are inevitable.

Aquatic Communities of Oligotrophic Lakes

There are several communities of plants and animals living in deep lakes. Those along the shore occupy a relatively small area or volume in proportion to the total area or volume of the lake, and their composition will be discussed later. In the deeper waters, one may find at least two distinct communities known as the limnetic and the profundal. The *limnetic* community exists in the region of open water of the epilimnion, down to a level known as the *compensation depth*—the depth at which plants manufacture as much oxygen in photosynthesis as they utilize in respiration. The depth to which light penetrates depends on many factors, including turbidity, color, and abundance of plants and animals in the water, as well as the intensity of light entering the water and the light-absorbing properties of water itself. For the most part, the occupants of the limnetic community are *plankton* —microscopic or near microscopic plants and animals so small that they are not able to determine the direction of their own travels. Their movements are thus subject to the physical movement of their environment. There may also be some swimming forms (*nekton*), such as fishes, and some surface dwellers (*neuston*), including algae and certain insects. The plant species of plankton (phytoplankton) are really the fundamental units of this community, for these minute plants—including diatoms, green algae, blue-green algae, dinoflagellates, and bacteria—provide the food for the animal part of the plankton (zooplankton) and ultimately, if indirectly, for all higher forms of animal life. Important groups of animals in the zooplankton include numerous protozoa, rotifers, and various minute crustaceans such as cladocerans, copepods, and ostracods.

The profundal community is found in the deeper waters of a lake, so deep that not enough light penetrates to enable the phytoplankton to manufacture more food than they consume. Inhabitants of this community include zooplankton, nekton, and certain forms which live on the bottom and are known as *benthos*. Compared to the life found in other types of lakes, the profundal community in oligotrophic lakes is relatively large in numbers of species and individuals. The cool oxygenated water allows the existence of animals such as lake trout, cisco, and a variety of invertebrates such as the amphipod, *Pontoporeia affinis*, the opossum shrimp, *Mysis oculata*, fingernail clams of the family Sphaeridae, and bloodworms of such genera as *Calospectra* and *Spaniotoma*. Each species has a maximum depth at which it may live, and there is great variation in the composition of profundal fauna from one lake to another as well as from one region of a lake to another (Welch, 1952).

Seasonal Changes in Oligotrophic Lakes

Certain fundamental seasonal changes have pronounced effects on the population of deep lakes, especially on the plankton whose members have short life cycles (Fig. 7-7). Winds blowing on a lake's surface are able to set the water in motion. In the spring, though not in the summer, the water of the lake is cool from top to bottom; there is therefore little temperature variation and hence little density, or viscosity, difference. The strong spring winds are able to stir the water from top to bottom, a phenomenon known as the spring overturn. This circulation supplies oxygen from the surface to the deeper levels of the water and distributes organic materials and other nutrients from the bottom throughout the lake. Accumulated toxic waste products may also be released and generally distributed.

The nutrients brought to the surface from the bottom, especially nitrogen and phosphorus, in co-action with the abundant oxygen and carbon dioxide and the warmer temperatures and increased light intensity of the spring season, are involved in the great increase of plankton which occurs in the spring. Since sufficient light for photosynthesis usually does not penetrate beyond 45 feet even in clear-water oligotrophic lakes, it is important that bottom materials be brought to the area where they may be utilized. An example of the significance of circulation of nutrients in a 159-foot-deep oligotrophic lake in Alaska is described by Juday et al. (1932). This lake, Lake Karluk, has a high plankton population owing in part at least to the enrichment of the water from decomposing salmon. The bottom sediments contain from 60 to 70 per cent diatom remains, which are high in silica, an element necessary for building the shells of these plants and thereby essential for high diatom populations.

The minute phytoplankton, especially diatoms, are the first organisms to show the spring increase in plankton (Fig. 7-11), and soon the animal populations which feed upon the phytoplankton, notably the copepods and cladocerans, also begin to increase in numbers. Although the plankton as a whole increases at this time, not all species experience a population increase simultaneously. The blooms (high populations) of individual species at different times indicate a complexity in the factors which govern the population dynamics of each species. That is, different species find the most suitable conditions for reproduction under varying circumstances. Thus some species of phytoplankton bloom relatively early in the season, when certain nutrients are available but the temperature is low and herbivorous zooplankton are scarce. Others bloom later in the season when nutrients are scarcer but temperatures are warmer and other factors more advantageous.

After some time (one or two months) the plankton populations decline, sometimes rather suddenly. Water at the surface has warmed rapidly, and there has been built up a large temperature gradient from the top to the bottom of the lake. The consequence of this is that the cooler, denser water of the bottom does not mix readily with the warm, light,

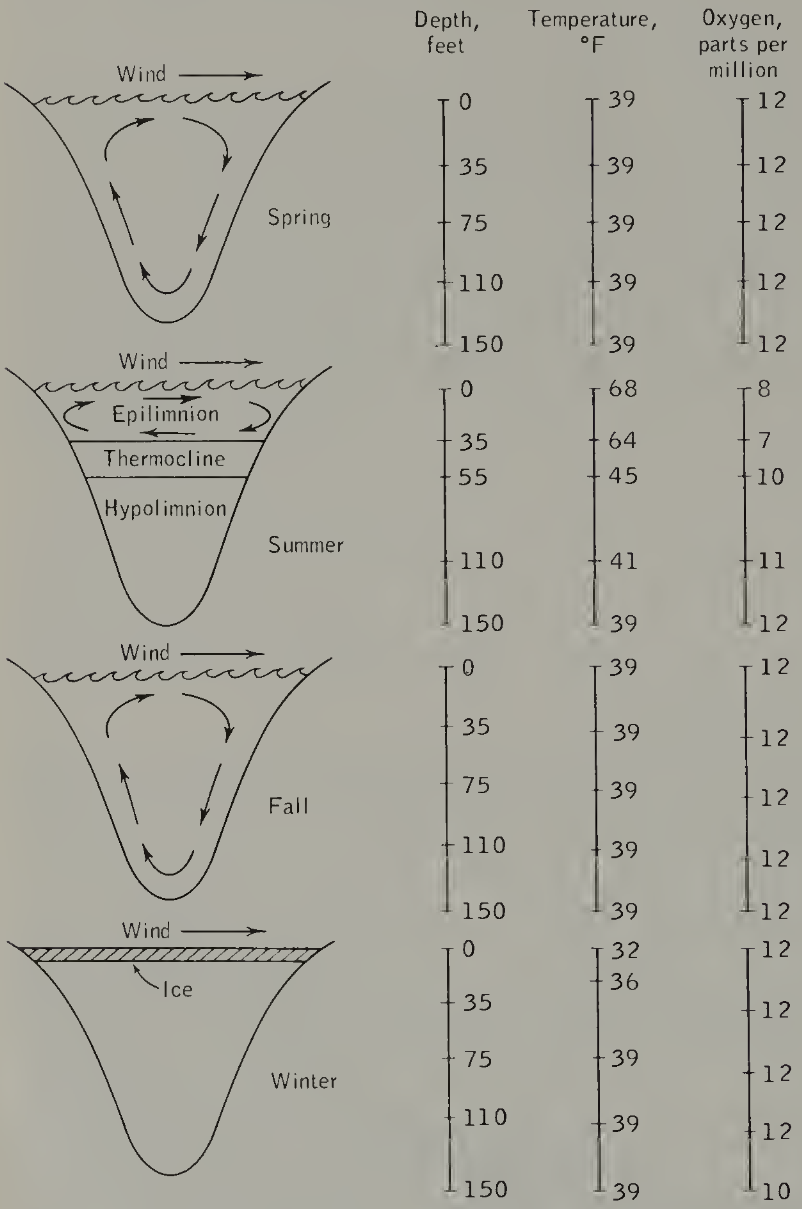

Fig. 7-7 Seasonal changes in a temperate oligotrophic lake. The temperatures and oxygen concentration at given depths are schematic. The exact temperature and oxygen concentration in any given lake at various depths will vary somewhat throughout each season, and each lake will exhibit variations from any other at any given time.

surface water. According to the thermal properties of water, the density of water increases rapidly from 4° Centigrade (to either higher or lower temperatures); a slight increase in temperature will decrease density (and hence resistance to mixing) rapidly. The upper layer of water is quickly warmed by the sun and consequently does not offer much resistance to mixing by the wind. However, as the temperatures of the water beneath this surface layer decrease even slightly with depth, the density and hence resistance to mixing increases rapidly. The sudden increase in density because of this small

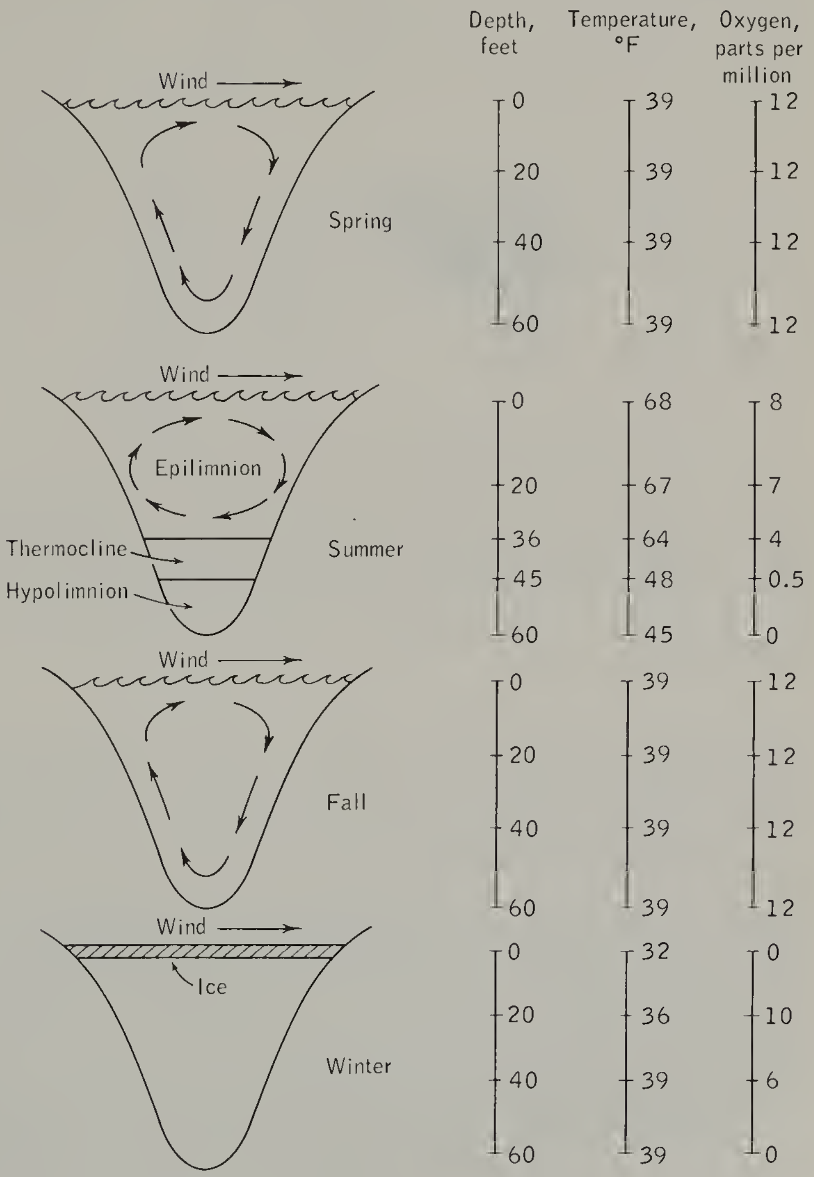

Fig. 7-8 Seasonal changes in a temperate eutrophic lake.

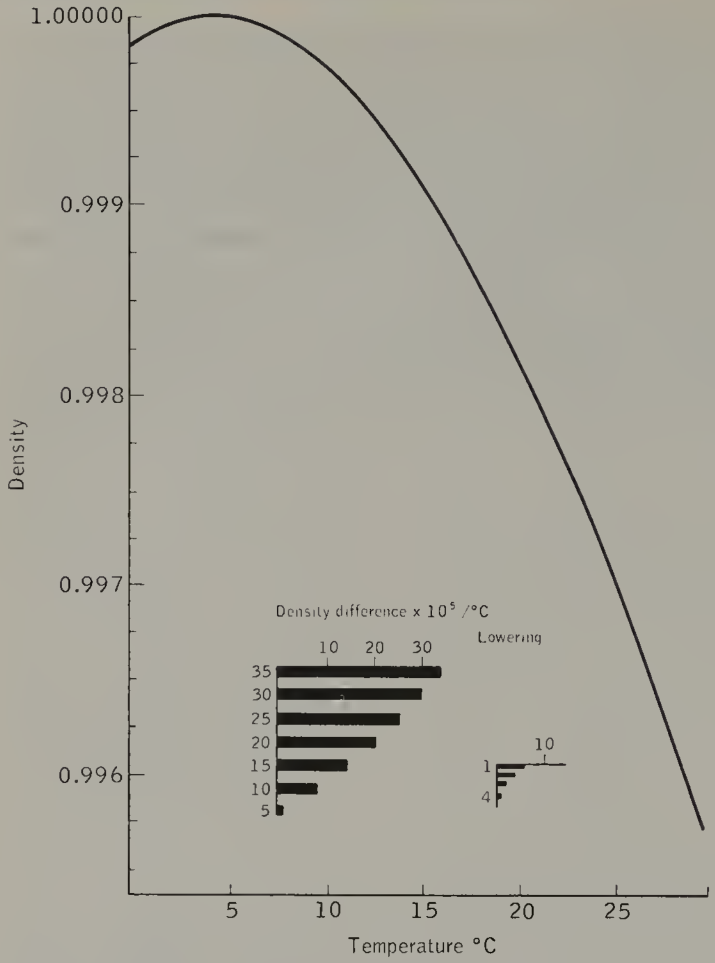

Fig. 7-9 Density as a function of temperature for distilled water. The density difference per degree Centigrade lowering is shown in the lower part of the figure for distilled water at various temperatures. From Vallentyne, J. R. 1957. The principles of modern limnology. *Am. Scientist,* 45:218–244.

difference in temperature tends to restrict circulation of water to the upper warm layer and thus makes it difficult for warming to progress downward. This leads to the establishment and maintenance of the thermocline and the consequent elimination of further mixing of the surface and bottom water. The water of the epilimnion continues to circulate, and the hypolimnion, although isolated, does not become depleted of oxygen. However, the epilimnion is now isolated from the bottom nutrients, and this may be one of the factors involved in the plankton decline in late summer (Fig. 7-10).

Although direct circulation of water by the wind is restricted to the epilimnion while the thermocline persists, there is some movement of water in the hypolimnion and thermocline. This movement is due to the effect of wind blowing in one direction, "piling up" epilimnion and thermocline water on the downwind (leeward) side of the lake, and depressing the hypolimnion under it. When the wind ceases, the water rushes back to the opposite side of the lake, and the hypolimnion is depressed on that side, meanwhile rising on the leeward side. It may take an hour to several days for one excursion of the wave across the lake and back, depending on the size of the lake. The wave causing alternate depres-

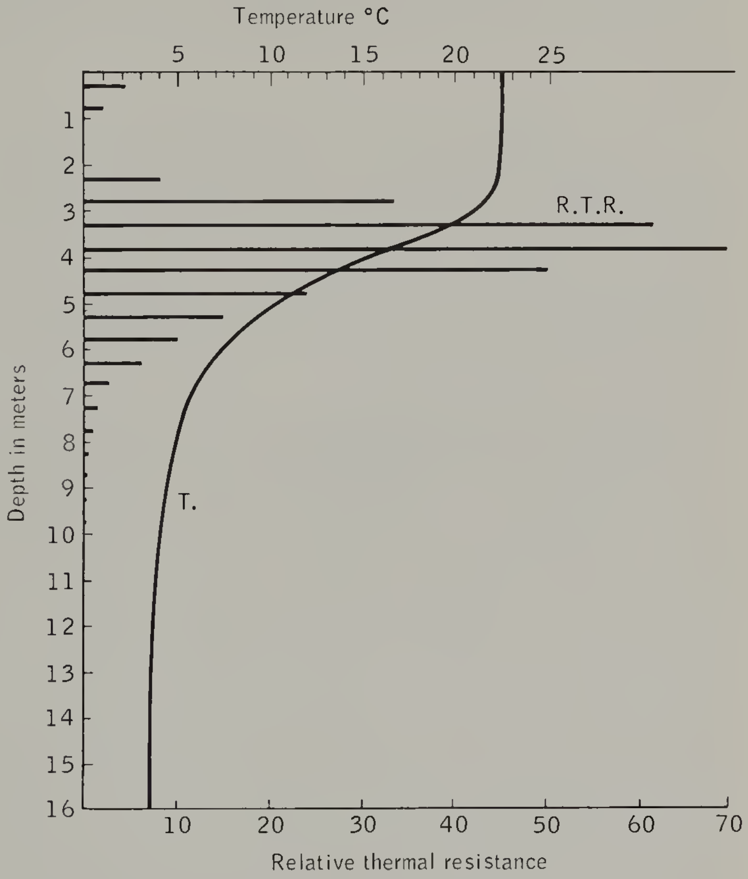

Fig. 7-10 A summer temperature profile (single line) and relative thermal resistance to mixing (bars) for Little Round Lake, Ontario. The relative thermal resistance (R.T.R.) to mixing is given for columns of water 0.5 meters long. One unit of R.T.R. = 8×10^{-5}, i.e., the density difference between water at 5° and 4° Centigrade. The R.T.R. of the lake water columns is expressed as the ratio of the density difference between water at the top and bottom of each column to the density difference between water at 5° and 4° Centigrade. From Vallentyne, J. R. 1957. The principles of modern limnology. *Am. Scientist,* 45:218–244.

sion and elevation of the hypolimnion continues oscillating back and forth across the lake about one or more nodes for some time (up to a week) after the wind has ceased. Although the surface of the water may be elevated only a fraction of an inch per mile of surface, the hypolimnion may be depressed a few yards per mile. There are many complications that may exist because of recurring winds, the size and bottom contour of the lake, the effects of the earth's rotation, and other conditions. Mortimer (1952) has studied these oscillating current systems (called *seiches*) extensively and points out that both the thermocline and hypolimnion are affected by such movements, which may alter the distribution of plankton and stir up an otherwise stagnant hypolimnion.

As fall approaches, the water on the surface and in the whole epilimnion cools. As it cools, the difference in density of the water of the epilimnion compared to that of the thermocline disappears. Strong fall winds are now able to circulate the water completely in the same manner as was done by the spring winds, and the thermocline (and hence thermal stratification) is destroyed. This fall overturn once again redistributes bottom materials, and frequently there are fall plankton blooms which decline as winter approaches.

With the coming of winter, the temperature of the whole lake is lowered. Large lakes may not freeze from shore to shore, but when freezing does occur, the water directly under the ice is the coldest, with the temperature increasing to 4° Centigrade at the bottom, the temperature at which water is heaviest (Fig. 7-9). In deep tropical lakes, the bottom temperatures may be only 20° to 25° Centigrade, since the bottom temperature cannot be lower than the average temperature of the air during the previous overturn (Vallentyne, 1957). Since oligotrophic lakes are fairly deep, the cold water holds sufficient oxygen for the life that might become imprisoned under the ice, and winter stagnation does not occur. If the lake does not freeze, the water may circulate throughout the winter. If it does freeze, the ice melts with the approach of spring, and circulation resumes. In either case, overturn in the spring will induce the plankton to increase.

Development from Oligotrophic to Eutrophic

As time passes, oligotrophic lakes will fill in by the two processes previously mentioned. Their sides may also be eroded away to some extent and thereby help to fill in the deeper parts of the basin. Exactly when a lake passes from the oligotrophic to the eutrophic stage is difficult to determine, for there is great variation of physical and biological conditions in lakes. One criterion that has been used to designate eutrophic lakes is that they possess a hypolimnion smaller than the epilimnion (Fig. 7-8). It is not always easy to use this criterion, however, since thermoclines may not develop every summer, especially in shallower lakes. When a thermocline forms, the hypolimnion may be so small and organic materials so abundant that stagnation occurs in the hypolimnion.

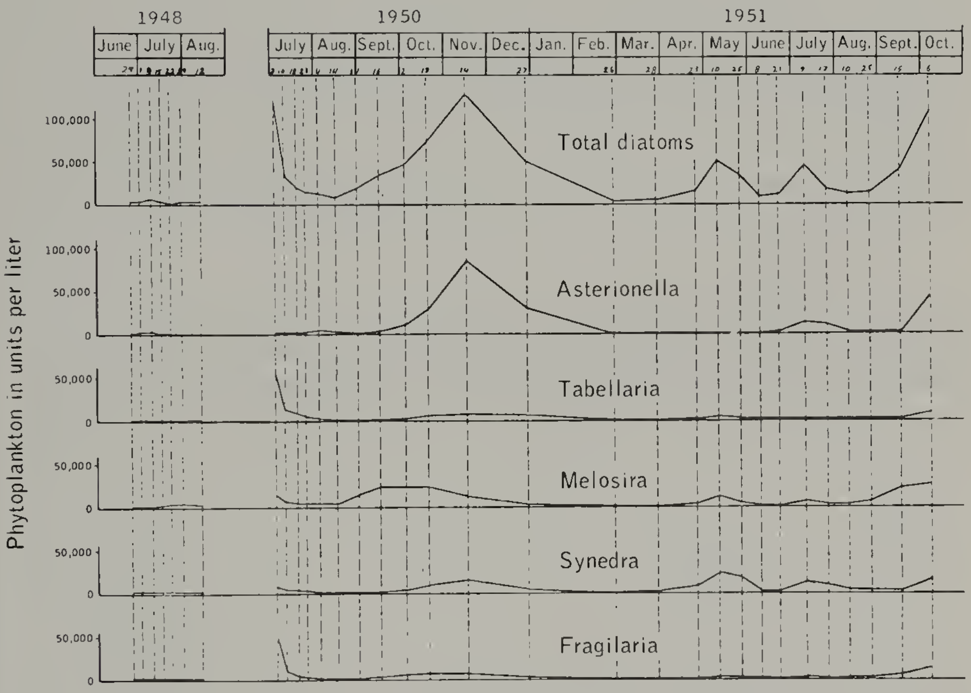

Fig. 7-11 Seasonal variation in standing crops of total diatoms and the major genera of this class in Douglas Lake, Michigan, during the summer of 1948 and from July 3, 1950 to October 6, 1951. Fall overturn began between September 16 and October 2, 1950. Ice appeared November 24, 1950; ice disappeared April 13, 1951. Thermal stratification began between May 10 and May 25, 1951. Fall overturn began between September 15 and October 6, 1951. From Tucker, A. 1957. The relation of phytoplankton periodicity to the nature of the physicochemical environment with special reference to phosphorus. II. Seasonal and vertical distribution of the phytoplankton in relation to the environment. *Am. Midland Naturalist,* 57:334–370.

Life and Seasonal Changes in Eutrophic Lakes

Life is abundant in eutrophic lakes, and plankton populations become especially high in the spring and fall (Fig. 7-12). In Clear Lake, California, Goldman and Wetzel (1963) found a large standing crop of phytoplankton, despite high turbidity and a consequent shallow penetration of light sufficient for photosynthesis (seldom below 12 feet). In this lake the spring phytoplankton productivity was not as great as the autumnal. Lakes may vary with respect to the dominant phytoplankton species present. Thus Tucker (1957) found in Michigan lakes that some were dominated by diatoms, some by golden algae, others by blue-green algae. Among the zooplankton of eutrophic lakes, rotifers may be the dominant type, as well as cladocerans, copepods, and protozoa. Since zooplankton feed on phytoplankton, their populations may be determined by phytoplankton populations, but probably in a complex way. For example, the rate at which certain species of copepods lay eggs in some lakes is related to the abundance of phytoplankton, but other past conditions probably affect egg-laying even more (Edmondson et al., 1962).

Organisms in the profundal zone may be numerous, but not very varied in species, especially in the oxygen-low hypolimnion. Thus in Lake Providence, Louisiana, where the profundal benthos is limited mainly to Chironomidae (midges), *Chaoborus* (phantom midges), and Oligochaetes (worms),

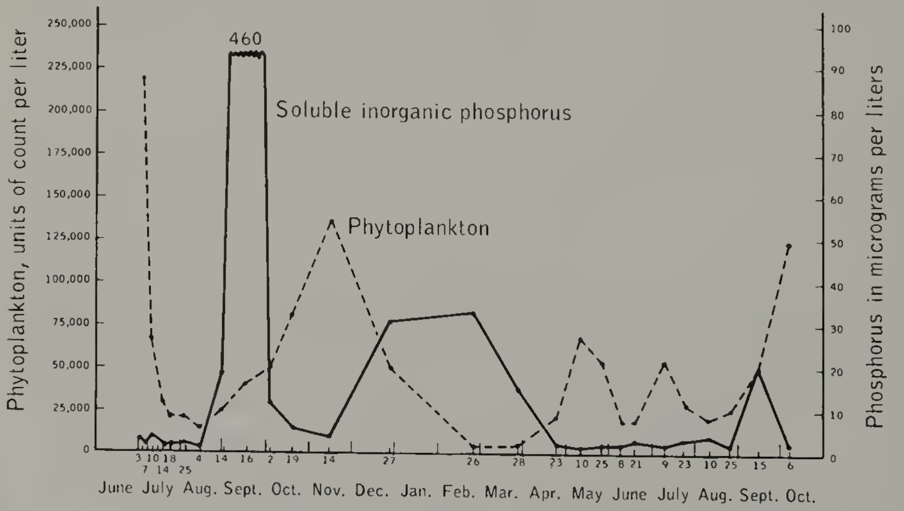

Fig. 7-12 Seasonal variation of standing crop of total phytoplankton and soluble inorganic phosphorus at 20-meter depth in Douglas Lake, Michigan. Years 1950–1951. See explanation of Fig. 7-11. From Tucker, *op. cit.*

Moore (1950) noted a high summer productivity as indicated by a standing crop averaging 90.4 pounds per acre. Typical fish of the profundal zone include pike, large-mouth bass, and catfish, and in the shallower areas bluegill, sunfish, and perch.

Of special concern to plankton of eutrophic lakes is the ability to maintain a certain position in the lake. Phytoplankton, for example, are able to produce food only in the upper levels where there is adequate light. If they descend too far, they will eventually die. Similarly, if zooplankton fall below their food supply (the phytoplankton), they will be in difficulty. Recalling what has been said concerning temperature and density gradients and the effects of thermal stratification on circulation of water in lakes will indicate the complexity of the problem. The situation is especially serious for plankton of eutrophic lakes because of the stagnation of the hypolimnion. The density of the protoplasm of plankton is such that the organisms tend to sink. However, certain devices either act as floats or increase friction to slow down sinking movements. Thus hairs, spines, attachment of individuals into colonies, air floats, and oil bubbles are among the various devices which help them stay in the limnetic community.

Some of the benthos in the profundal zone have solved the flotation problem remarkably well. These animals exist as members of the benthos only during the day, rising to the surface in the limnetic zone by night. Thus Woodmansee and Grantham (1961) found that in Lake Geiger, Mississippi, the majority of the population of *Mesocyclops edax*, a copepod, and *Chaoborus albatus* spent daylight hours in the oxygen-deficient hypolimnion, and at night both populations moved into oxygenated water.

In eutrophic lakes, the thermocline may become established in early May and remain until mid-September, as in Lake Douglas, Michigan (Tucker, 1957), and Lake Providence, Louisiana (Moore, 1950). The upper limit of the thermocline may descend 9 to 15 feet during the summer, depending on the geographical location and physical conditions of the lake. As this occurs, the hypolimnion becomes smaller, since the thermocline does not usually vary in thickness this much. Oxygen may be thoroughly depleted by July as bacteria use it in decomposing dead organisms, and animals use it in respiration. After the oxygen has been used up, phosphorus, nitrogen, and other nutrient elements are slowly released from iron compounds on which they were formerly adsorbed or united with chemically. Since it may take up to eight weeks for this release to be completed, the sooner oxygen is depleted, and the longer the thermocline lasts, the more complete will be the release of the minerals into solution in the hypolimnion (Tucker, 1957). The greater the amount of minerals that are released, the larger may be the plankton bloom when overturn once again brings these substances into the limnetic zone. However, in Douglas Lake, when the overturn occurs, phosphorus does not increase in the upper water. Although there are several possible explanations for this anomaly, none are fully satisfactory (Tucker, 1957).

The fall overturn will bring an upsurge in the plankton bloom, which will decline with the approach of winter. If eutrophic lakes freeze over, the situation of aquatic organisms becomes grim. With a smaller total volume of water than the oligotrophic lake and a much higher total population of organisms, oxygen may become extremely scarce. If the ice cover remains for a long time, especially if a cover of snow prevents light penetration and photosynthesis is thus reduced, great destruction of life may occur. Decomposition of the abundant organic matter in the water and on the bottom adds to the difficulties by further depleting the oxygen supply, although some oxygen is being continually added by phytoplankton and rooted plants of the shore zone. When spring arrives, the overturn again allows the entire lake to benefit from the nutrients on the bottom and the oxygen from the atmosphere.

Development of Eutrophic Lake to Dry Land

As eutrophic lakes continue to become shallower, they reach a point at which thermoclines never form, and circulation occurs throughout the summer. The entire volume of water may become quite warm at this time. Rooted aquatics usually become established, even in the deepest parts of the lake (Fig. 7-14). This stage of vegetation-choked water, sometimes called the *senescent* stage, is highly productive. Small fishes, frogs, water snakes, and turtles may abound, as well as a host of insects and other invertebrates (Fig. 7-13).

When the senescent lake becomes shallower, it may become a pond; that is, merely a smaller area of open water. Or it may develop directly into a swamp or marsh. A swamp is usually considered to contain trees, while a marsh, by definition, does not. Ponds may become so shallow that they dry

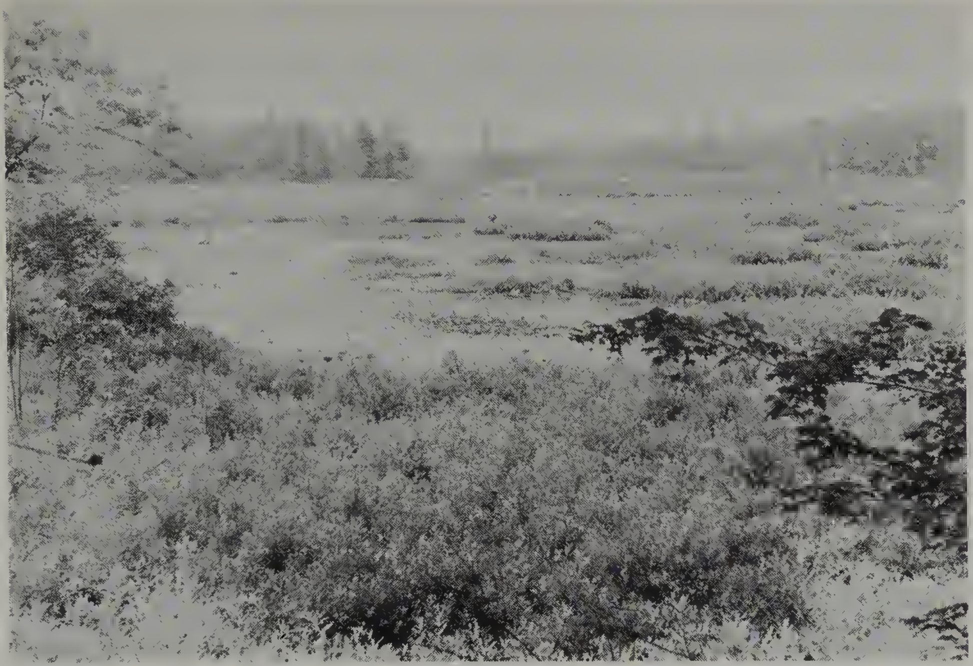

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Fig. 7-13 A lake in the senescent stage with emergent vegetation growing throughout. Near Petersham, Massachusetts.

up in the summer months, thus becoming temporary ponds (Fig. 7-15), unsuitable for occupation by permanently aquatic animals. Because of this major change in environment, forms of life are more limited, although many insects and other animals may be common. Plants growing here are predominantly emergents (plants which live with their roots submerged in water but whose vegetative and flowering parts are mostly above the water). Cattails, arrowheads, pickerel weeds, and various kinds of sedges and rushes are among the most abundant of them. Certain invertebrates are of interest because they are found in temporary ponds. Among the widely distributed members of this group are the fairy shrimps of the genus *Eubranchipus*. Some relatives of this genus are able to live in temporary alkaline or saline pools in the West. Because of the temporary nature of these ponds, many of the larger predatory species are absent.

Eventually the pond, marsh, or swamp will dry up completely as terrestrial plants and animals invade the site of the former lake. Bushes, trees, and herbaceous plants which are tolerant of soggy ground will add their remains to the soil, until conditions become sufficiently mesic to tolerate a purely

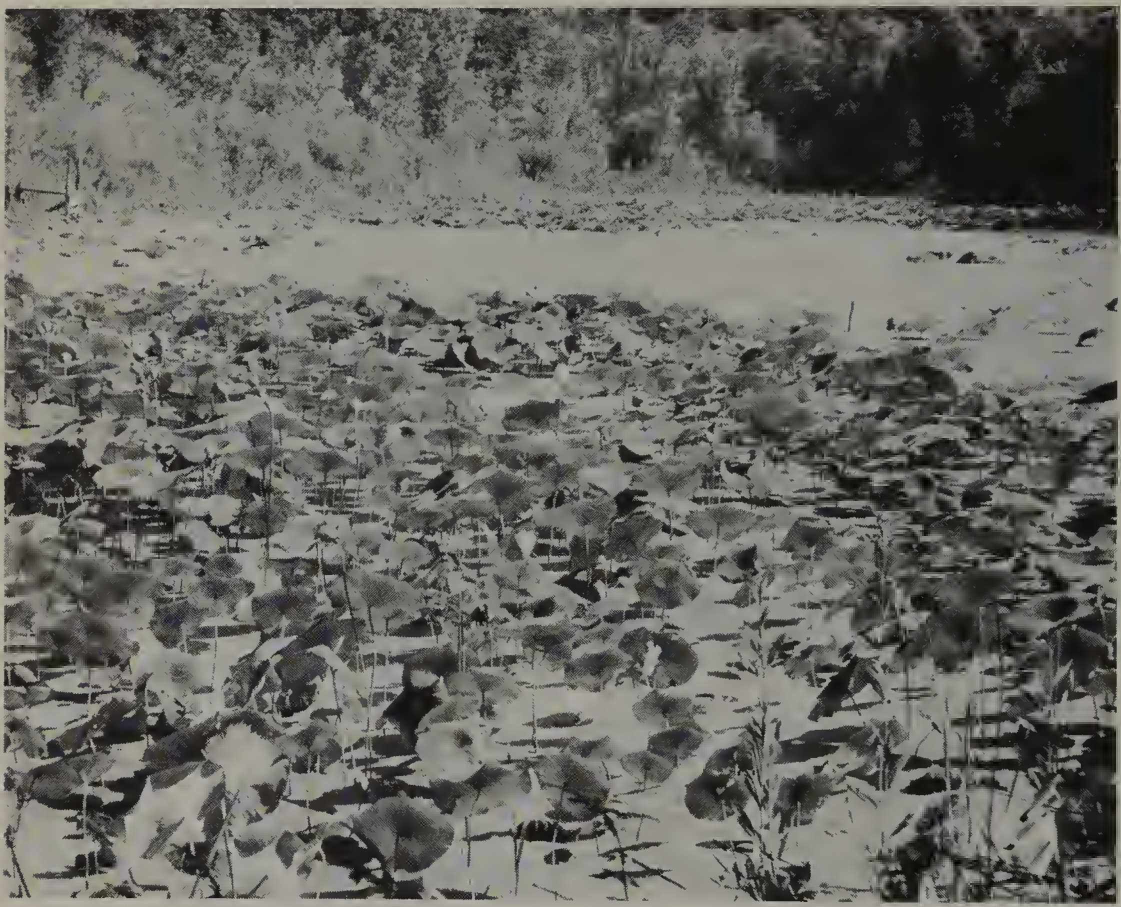

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Fig. 7-14 Vegetation-choked stage of a eutrophic lake. The large plant is the lotus, *Nelumbo lutea.* The water around these plants is covered by duckweed, *Lemna minor.* Macoupin County, Ill.

terrestrial community. Finally, the end of the eutrophic-lake succession is the terrestrial climax community (Fig. 7-16).

Conditions in Dystrophic Lakes

Dystrophic lakes proceed along a different line of succession. They are frequently formed as the result of glacial action similar to that which forms some oligotrophic lakes. Owing to physical and chemical states which prevent the decay of organic materials, biotic conditions in such lakes are different, and succession takes a different course. Calcium and oxygen are usually deficient, and the pH of the water is generally low. The abundant organic matter of the water is in the form of undecayed organisms which create deposits of peat

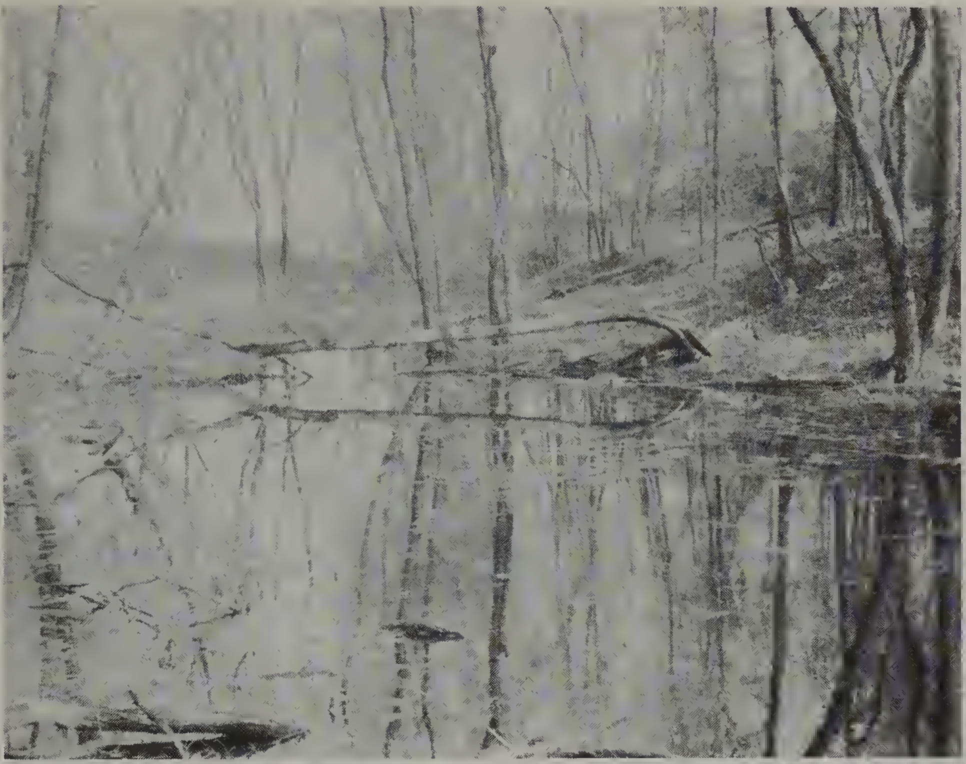

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Fig. 7-15 A temporary pond which will dry up completely during the summer. In spring it serves as a home for the fairy shrimp, *Eubranchipus*, and as a breeding place for amphibians. Macoupin County, Ill.

on the bottom and frequently impart to the water a brown stain.

Dystrophic lakes are usually poor in numbers and types of organisms. Larger plants, e.g., *Chara*, which remove calcium from the water, may be present, but in general the phytoplankton and rooted aquatics are scarce. Zooplankton may be numerous, but larger invertebrates are frequently low in abundance, as are such vertebrates as the fishes. Sphagnum moss is the typical plant found growing in the beach or shore (psammolittoral) zone of these lakes, along with sedges and other plants which form a mat.

Development of Dystrophic Lakes to Dry Land

As the dystrophic lake accumulates peat on the bottom, it hastens its own end. The sphagnum and rooted vegetation of the shores may grow out into the water, advancing over the surface of the lake. It is thereby developing into a peat bog,

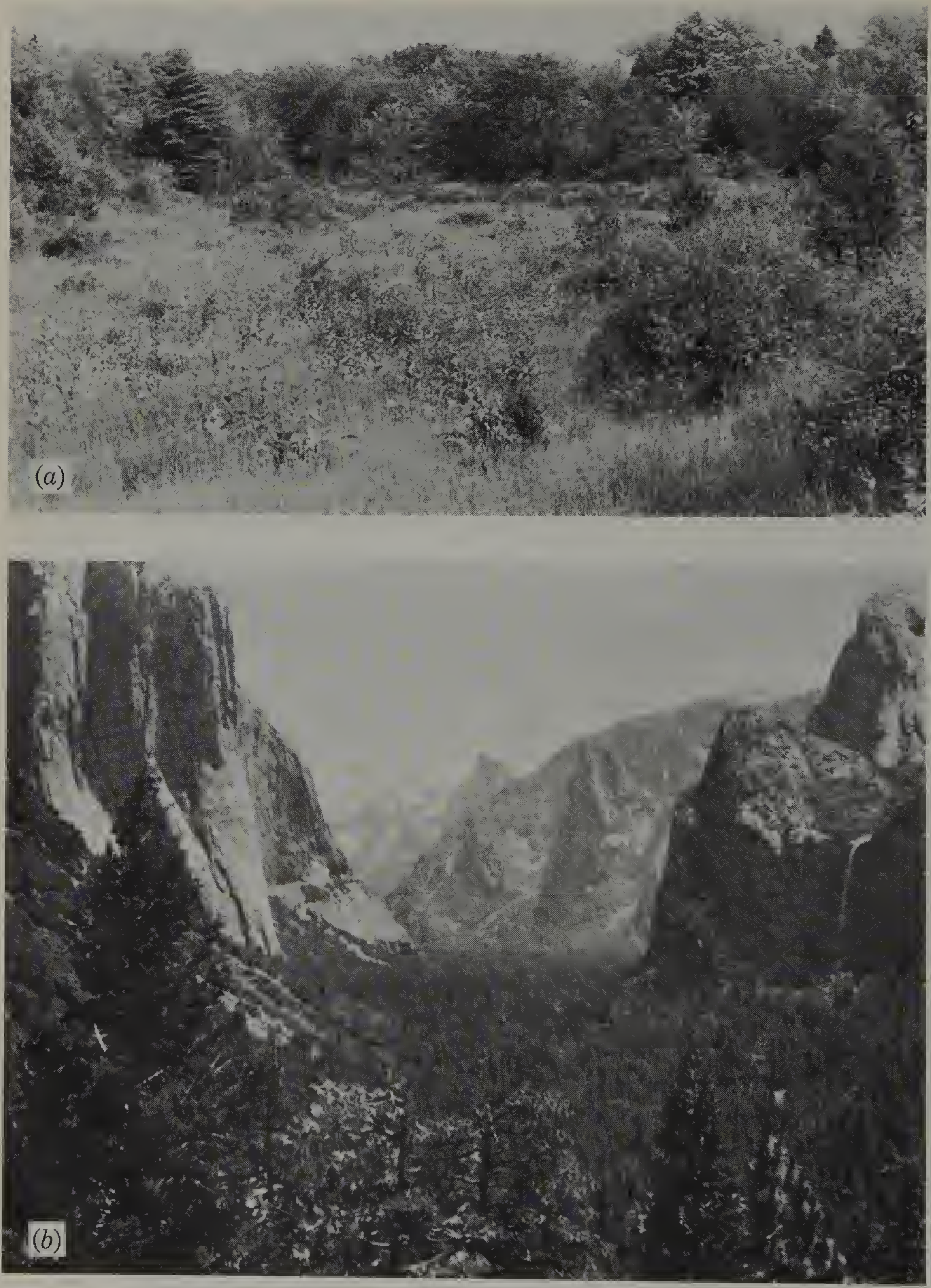

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Fig. 7-16 Terrestrial succession on the site of former lakes: (*a*) Early stages of succession in a moist area which has not been long dry. (*b*) A coniferous forest on the site of a former glacial lake, Yosemite Valley, California.

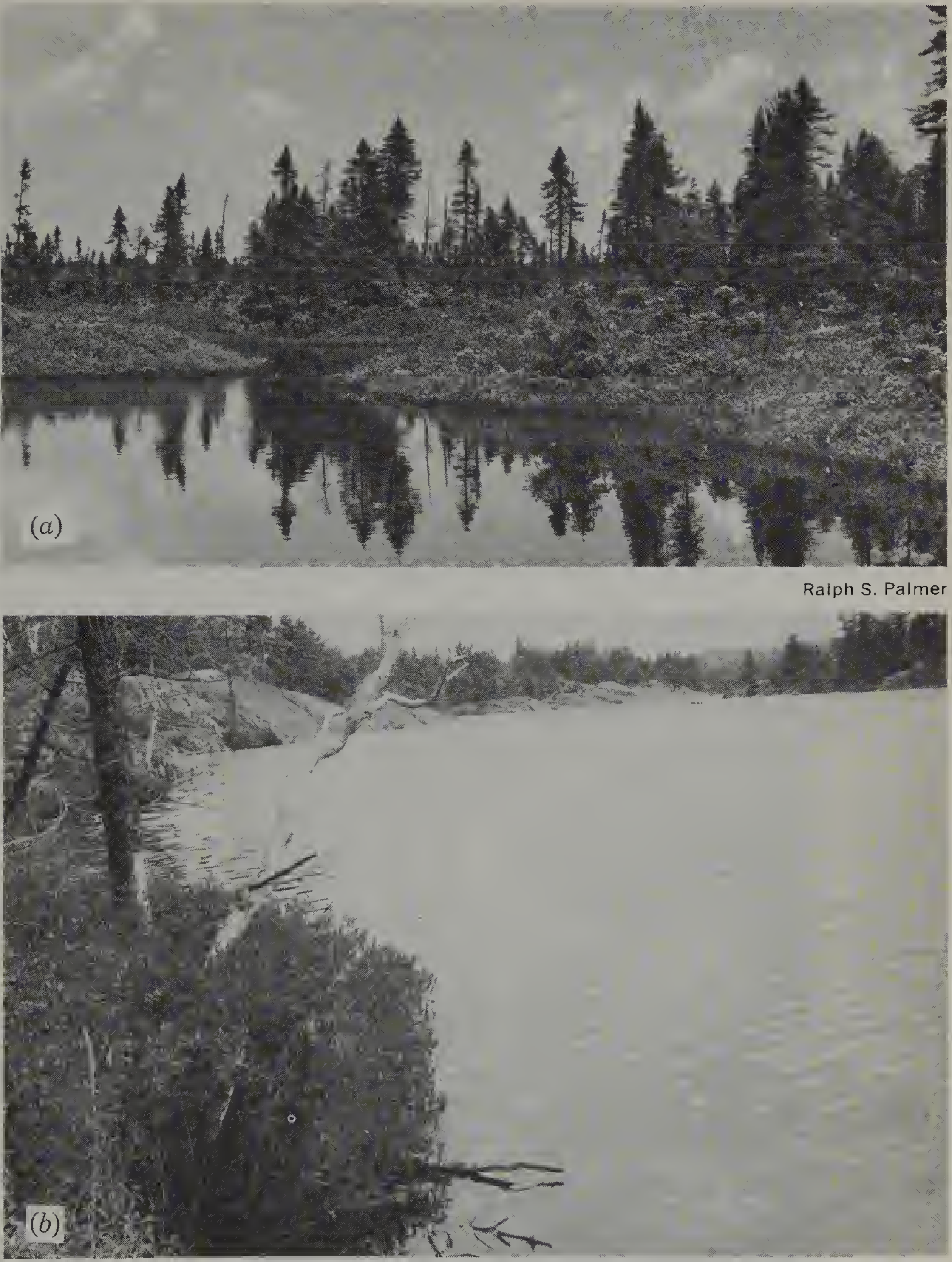

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Fig. 7-17 Development of dystrophic lakes:

(*a*) A dystrophic lake in Maine in the pond stage, with quaking mat well out over the water.
(*b*) A dystrophic lake in Ontario, Canada, in early stage of succession. A vegetation mat is just beginning to grow out over water at left.

with a shore of vegetation forming a quaking mat, and a bog lake in the center (Fig. 7-17*a*, *b*).

The surface mat eventually closes over the bog lake, and sphagnum and other vegetation fill up the basin. The outstanding physical condition of such a community is the low pH of the saturated "soil" of the mat, which is sometimes less than 4.0. A variety of plants are especially adapted to these conditions of moisture and low pH, and these make up the bog community. Here we find the insectivorous pitcher plants (*Sarracenia*) (Fig. 7-18) and sundews (*Drosera*); cranberry (*Vaccinium oxycoccus*) and cotton grass (*Eriophorum*) (Fig. 7-19). Shrubs which invade the bog usually include leatherleaf (*Chamaedaphne*), Labrador tea (*Ledum*), and bog rose-

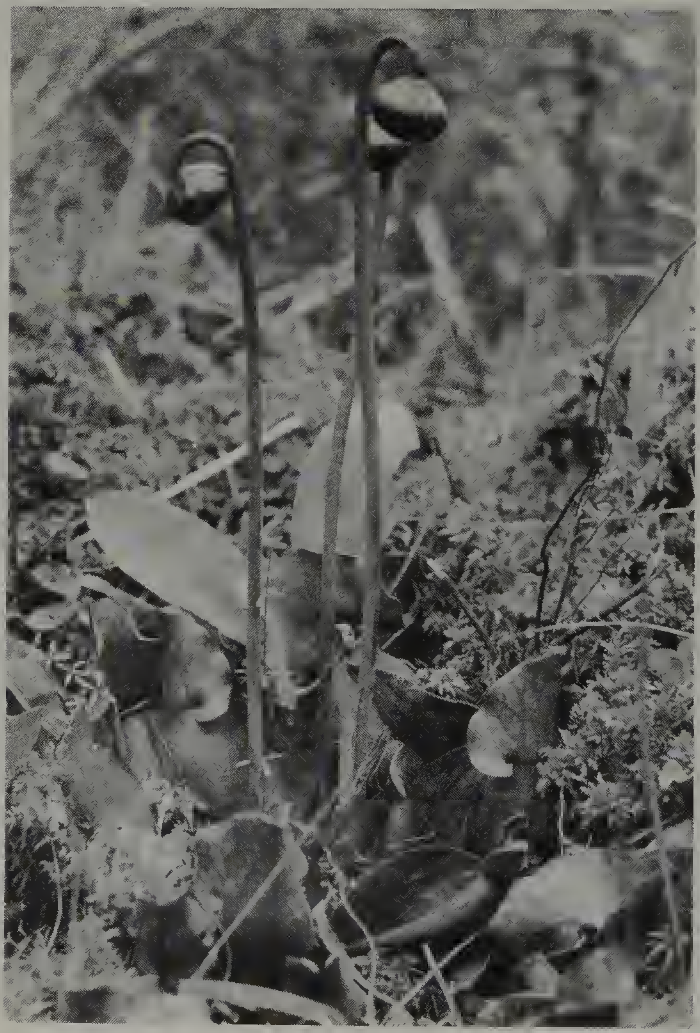

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Fig. 7-18 Typical bog plant, the pitcher plant, *Sarracenia purpurea*.

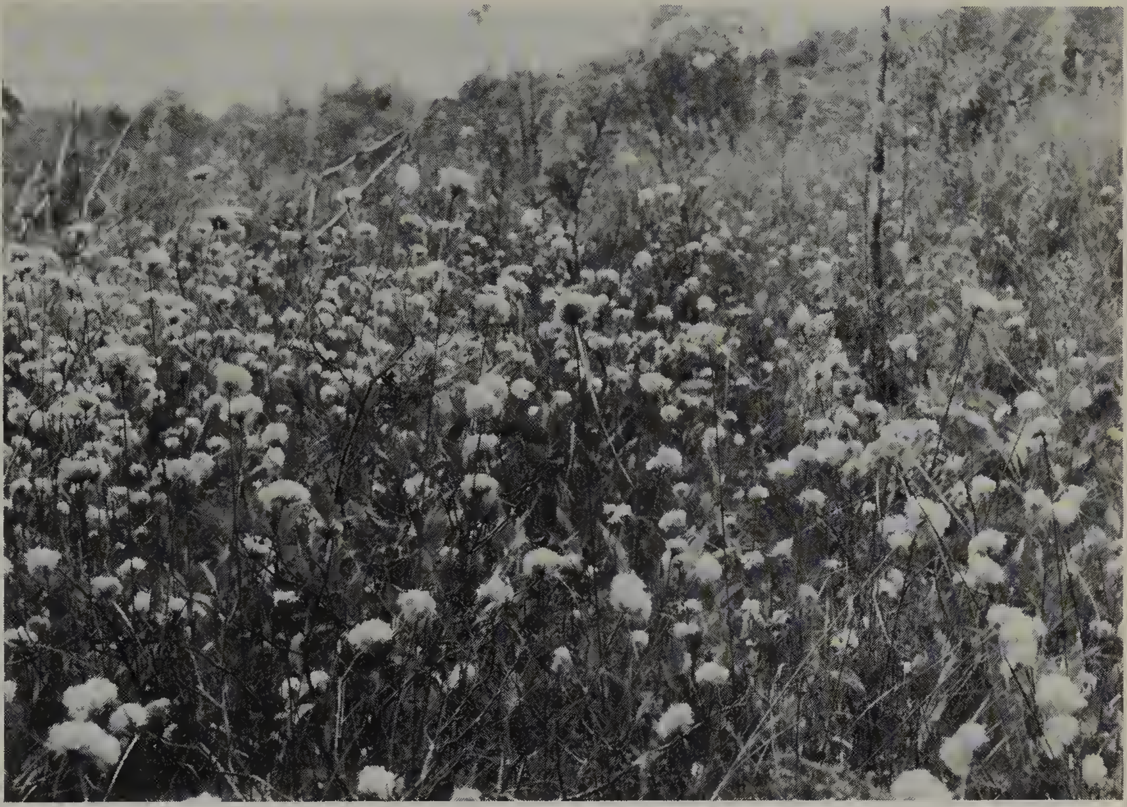

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Fig. 7-19 Cotton grass, *Eriophorum*, a typical genus in northern and arctic bogs, here growing in a marsh in western Maryland at an altitude of about 3,000 feet.

mary (*Andromeda*). Several species of orchids are restricted to this habitat. Diatoms and certain species of algae may be found among the saturated sphagnum.

Eventually the basin will be further filled by encroaching bushes and by the dead bodies of plants and animals, until finally the terrestrial climax community covers it. The length of time required for this to occur varies widely, depending on such variables as the original depth of the basin, its drainage, and other physical conditions which affect the growth of organisms and the rate of sedimentation. As in the succession of oligotrophic lakes, a series of communities has been established and changed, each one replacing the preceding one, until eventually the climax is reached.

ZONATION OF AQUATIC COMMUNITIES

Along the edges of eutrophic, oligotrophic, and senescent lakes, there may be shores which descend gradually to the depths of the lake, with bottoms of sand, mud, gravel, or clay. Frequently aquatic vegetation will be found growing here, and a whole series of communities may be formed. Floating aquatics will occupy the deep water, and various kinds of rooted vegetation will follow in regular sequence up to the beach. These communities show a zonation similar to that of vegetation on a mountain, except that it occurs for a much shorter distance and is therefore more easily observed. In effect, this zonation illustrates the process of succession in lakes. It is possible to observe from it how lakes become more shallow by the action of such communities and how the changing depth of the water affects the composition of the communities.

Small Floating Aquatics

The areas of lakes involved in zonation include the littoral zone (the region in which there is light penetration to the bottom) and the psammolittoral zone (the region along the edge of the water). The deepest water of the littoral zone may have a surface cover of small floating plants such as the duckweeds—*Lemna*, *Wolffia*, and *Spirodela*. Sometimes these plants will cover a small lake or pond (Fig. 7-20). Of course, in this region as in most of the succeeding ones there are plankton and nekton populations. Where the water is shallower, perhaps 20 feet or less, some rooted aquatics may be found, including *Vallisneria*, *Anacharis*, *Myriophyllum*, and *Ceratophyllum*. These are all totally submerged plants. One of the largest and most abundant groups of submerged aquatic plants found in the littoral zone belongs to the genus *Potamogeton*, which includes more than 50 species in North America.

Rooted Floating Aquatics

As the depth of the water decreases toward the shore, a zone containing a community dominated by rooted floating aquatics will be found (Fig. 7-21) Typical of such plants are white water lilies (*Nymphaea*), the cow lily (*Nuphar*), and *Potamogeton natans*. Many animals are associated with these

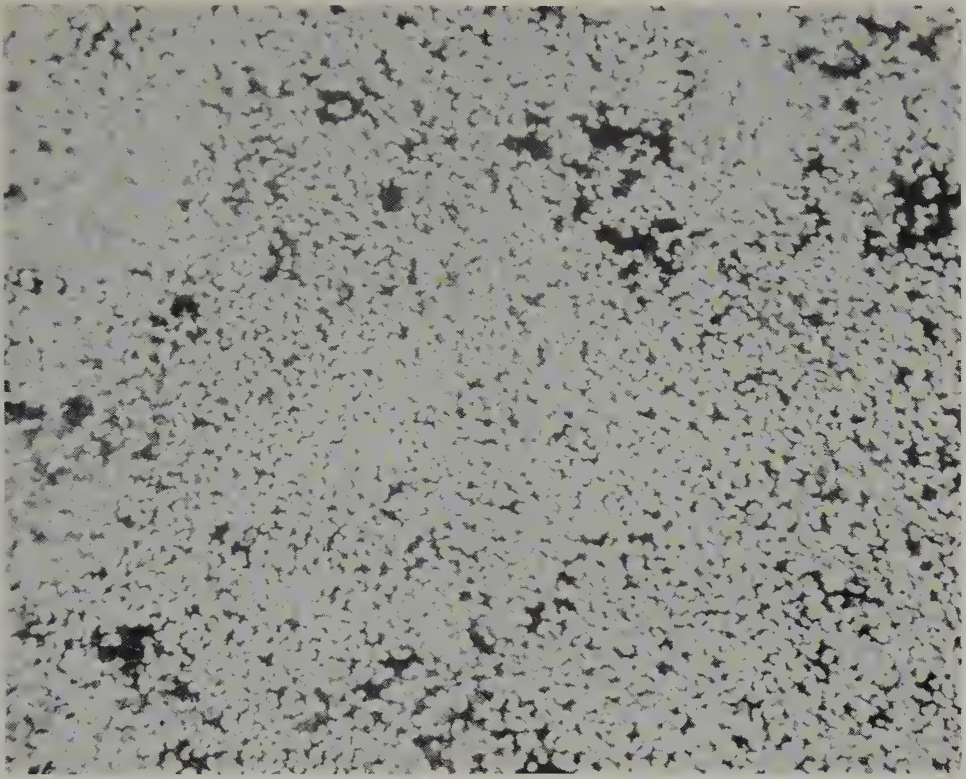

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Fig. 7-20 Duckweed, *Lemna minor,* covering the surface of a pond.

plants, using them as places for support as well as for food. Many herbivores feeding on the phytoplankton are present, while carnivores are there to feed on the herbivores. For example, the small fresh-water coelenterate *Hydra* may often be found hanging downward from the undersurfaces of pond lily pads. This little animal extends its tentacles into the water to catch small water animals such as insects, copepods, and cladocerans. These in turn feed on protozoa, bacteria, and minute algae (Pennak, 1953).

Emergents

In shallower water, a zone may occur possessing a community dominated by emergent plants. These species have their roots and lower stems in water, but most of the plant projects into the air. Some of the more common species of this community are cattails (*Typha*) (Fig. 7-22), bulrushes (*Scirpus*), reed grass (*Phragmites*), and wild rice (*Zizania*). In this zone the bottom is usually abundantly covered with the

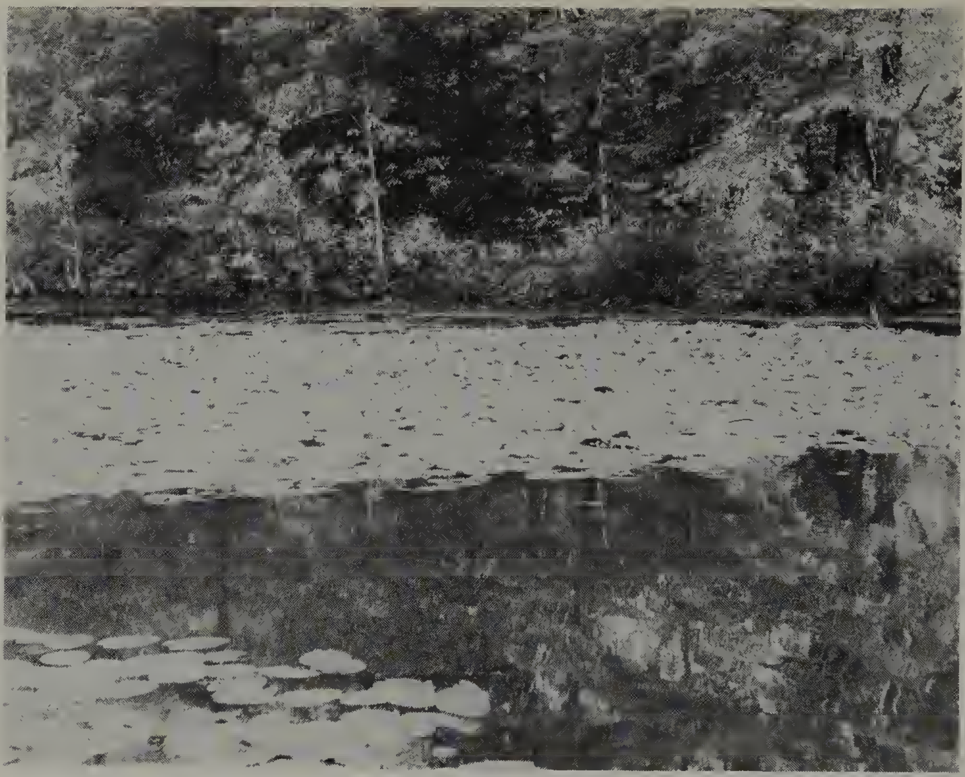

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Fig. 7-21 Zone of rooted floating aquatics, white water lilies, *Nymphea odorata*, and cow lily, *Nuphar advena*. Lake Huron, Canada.

rotting organic debris of the old emergent plants, and this forms a situation favorable to small animals. Insect larvae such as dragonflies, damsel flies, and adult and larval beetles and bugs may abound in the mud and water, along with a rich zooplankton. Larger forms such as frogs, salamanders, turtles, and water snakes may inhabit this community. Certain fishes like the bullhead (*Amieurus*) and the mud minnow (*Umbra*) are often present.

Saturated-soil Regions

Next to the shoreline, there is frequently a region in which the soil is saturated with water. Here a community exists in which the dominant plants are various sedges (*Carex*), rushes (*Juncus*), smartweeds (*Polygonum*), and many others (Fig. 7-23). This community may have a large number of microscopic plants and animals, so that the water edge, or psammolittoral zone, may possess the most densely populated community of all the zones.

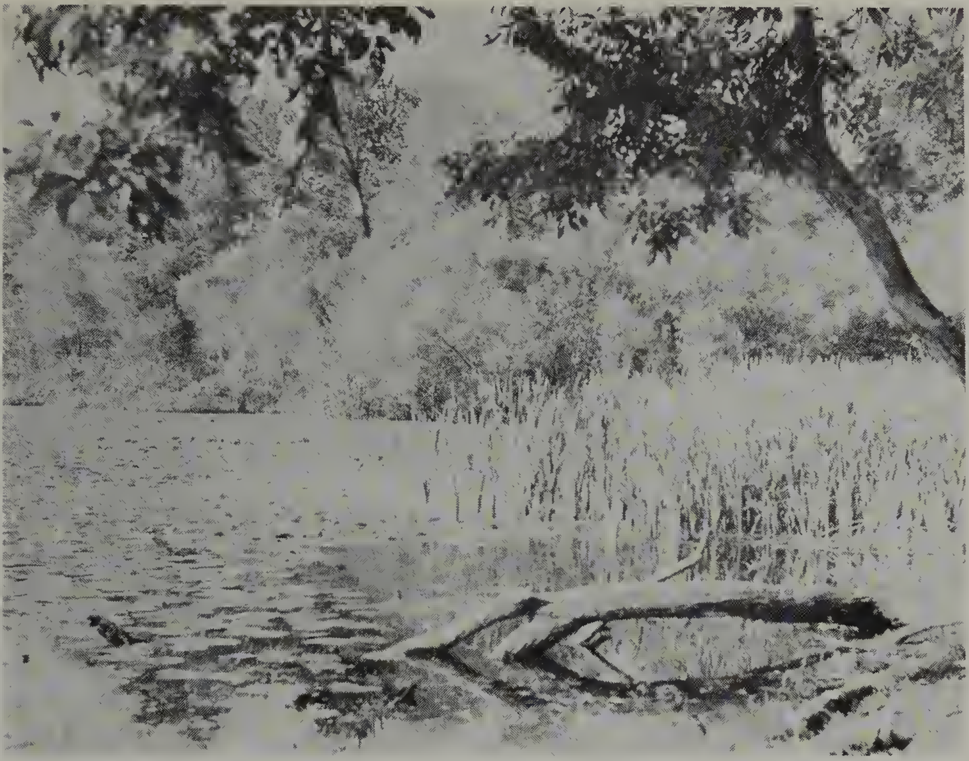

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Fig. 7-22 Floating rooted aquatics, *Nymphaea odorata;* emergents, here mostly cattails, *Typha*, advancing toward the center of the pond. Albany, N.Y.

Shore Communities

On drier land, farther from the shoreline, is a community dominated by rank herbs. Water is still abundant in the soil. Wild hemp (*Cannabis*), sunflowers (*Helianthus*), jewelweed (*Impatiens*), joe-pye weed (*Eupatorium purpureum*), and boneset (*Eupatorium perfoliatum*) may be among the common plants (Fig. 7-24). Animals are those of the terrestrial communities which can forage into the wetter locations. Common species include field mice, shrews, raccoons, and weasels among the mammals, various nesting birds (Fig. 7-25), and frogs and snakes among the lower vertebrates. Hordes of insects also constitute an important part of the community. Still farther back on land will be found the shrub community, with elderberry, red maple, box elder, cottonwood, willows, alder, and viburnum among the forms represented. A few shrubs such as the buttonbush may grow in more aquatic situations, but these are scanty. From the shrub stage, the development to the climax community will be a sere similar to

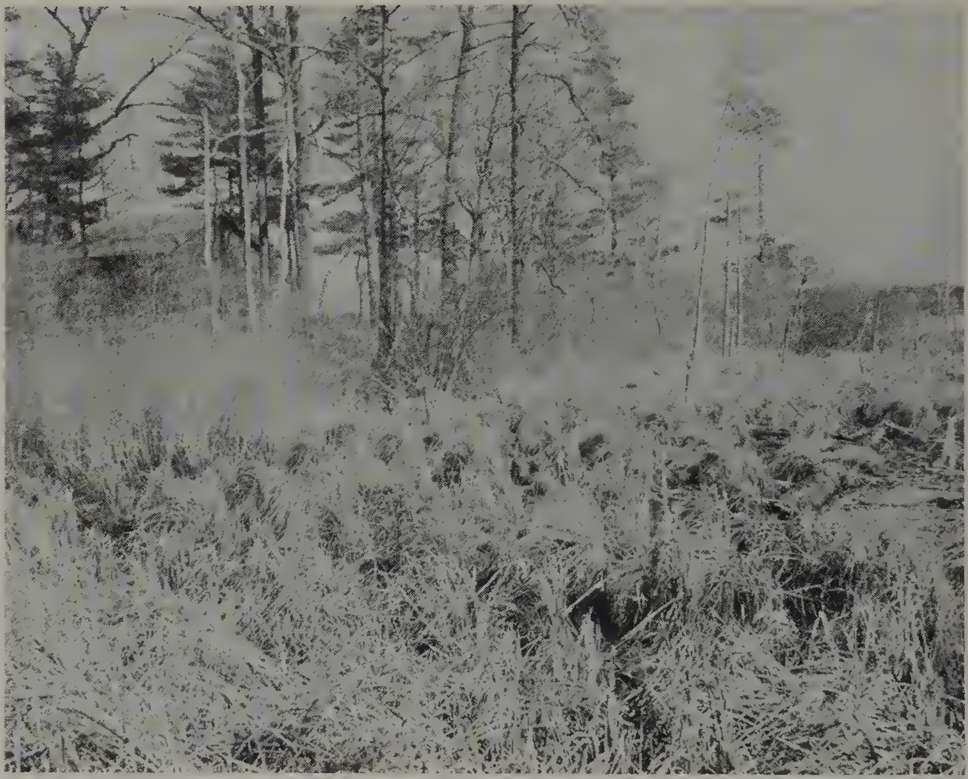

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Fig. 7-23 The region of saturated soil around the shore line of a pond, with sedges as the dominant plants.

the one described for terrestrial succession, with perhaps different dominants appearing in the various communities.

Evidences of Succession

The communities from the open water of the lake or pond through the littoral region to the climax on the shore may all be seen at one time; but they represent dynamic changes, which will eventually result in the filling in of the lake and the elimination of the communities. As time passes, each community will invade its neighbor toward the center of the lake. In all the communities, organic matter and silt are constantly accumulating, decreasing the depth of the water. With this change of environment each community invades the one next to it in deeper water and is in turn invaded by the one behind it in shallower water. Thus, as the filling process occurs, the submerged aquatic plants will be displaced by the floating rooted aquatics, and these by the emergent aquatics. As succession continues, the emergents will be replaced by

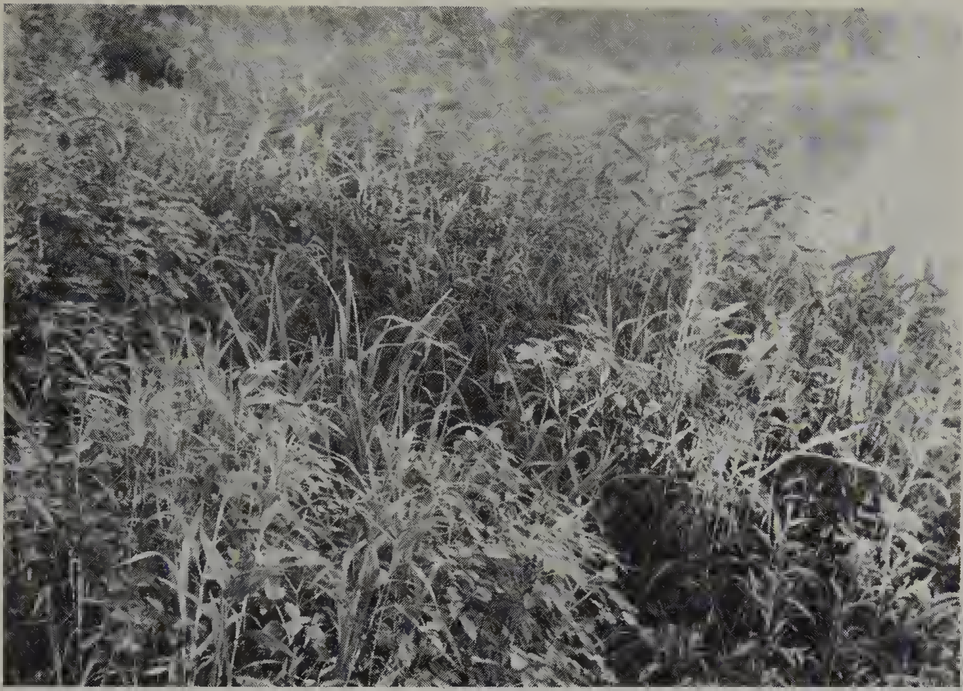

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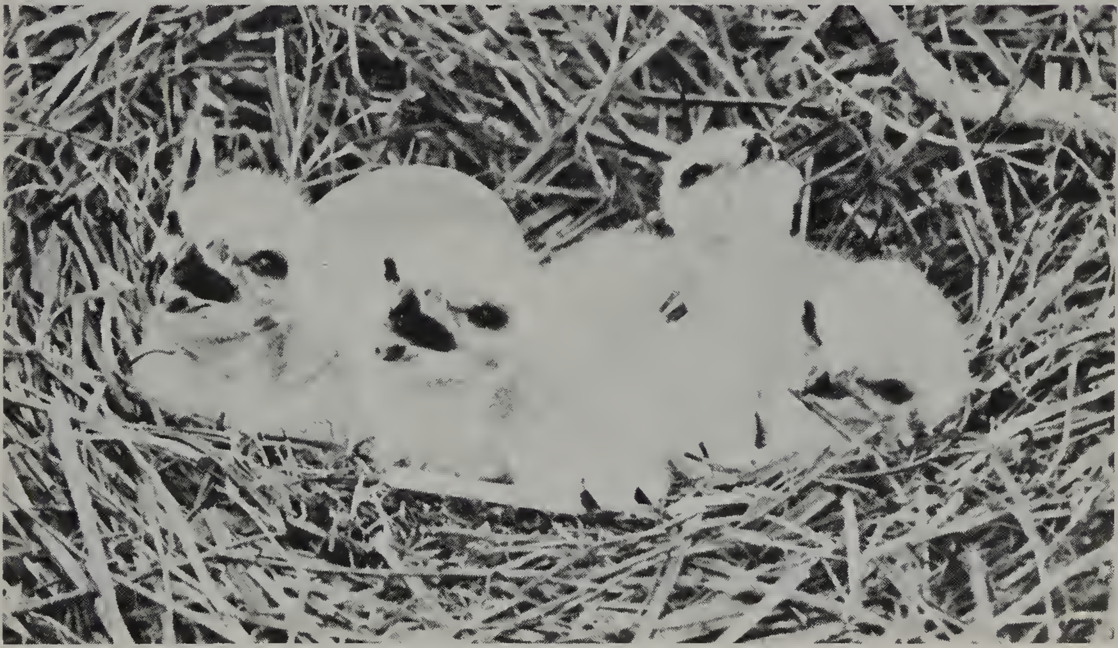
Fig. 7-24 Rank vegetation in the damp soil near the edge of a pond. Jewelweed and smartweed are dominants.



E. G. Tabor

Fig. 7-25 Marshes are nesting sites for many birds. Grassy marshes are preferred breeding habitat for the marsh hawk, *Circus cyaneus,* whose young are shown here in the nest.

sedges and rushes, and these in turn by rank herbs and shrubs. Gradually the terrestrial communities will move in where once there was open water, until finally the terrestrial community climax occupies the area.

The communities of plants and animals in the sere are similar in various kinds of lentic environments, although the species may vary. For example, muddy bottoms may support different plants and animals than gravel bottoms, and on shore the species found on sandy beaches may be different from those on rocky beaches (Fig. 7-26). Thus the species composition of similar communities will vary with different environmental conditions, but the general pattern of the succession will be about the same.

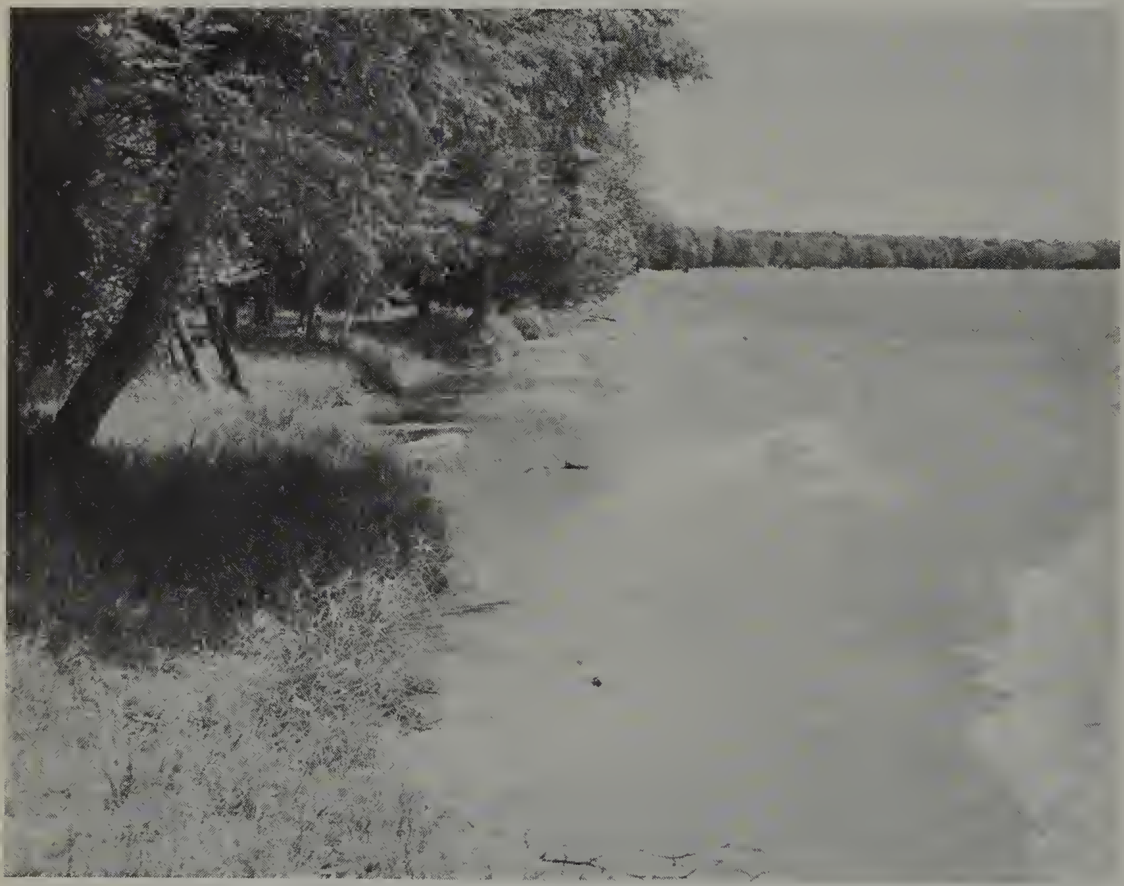


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Fig. 7-26 Sandy beach on a wave-swept shore. Notice that there is no large aquatic vegetation. Higgins Lake, Mich.

STREAM SUCCESSION

The development of streams is quite different from that of lakes and other lentic environments. Whereas in the succession we have reviewed above, organisms help to bring about the successional changes to a great degree, in lotic environmental evolution, physical forces play the dominant and almost exclusive role. Since physical forces, therefore, shape the development of biological communities in streams, the physical evolution of streams will be considered first.

Stream Gradient

In a flat world there would be no streams, for the water in streams is flowing from an area of higher elevation to an area of lower elevation, and ultimately to the sea. The difference in elevation from the origin of a stream to its terminus, divided by the distance it travels between these two points, gives the average elevation gradient of the stream. The greater the gradient, the greater should be the rate of flow, all other factors being equal.

When a land mass is newly elevated, the water will run off the surface into the natural depressions which are present and eventually find its way to the ocean. At first, many of these depressions may hold water as ponds or lakes, but with their filling and the erosion of their outlets, they tend to be obliterated. At the same time, the streams may be small and, if the elevation gradient is large, proportionately swift. Such a swift stream is able to carry or move large rocks as well as gravel and silt from the hills to the plains. This load, combined with the washing action of the water, will wear down the stream bed as its smaller tributaries are wearing down their stream beds and the surrounding hills. In effect, the hills are being slowly carried to the sea. As this occurs, the stream at any given point becomes larger, the stream bed lower, and the stream as a whole longer. Another result is that the elevation gradient is decreased and the flow slackened at any given point along the stream, a process called *base leveling.*

As long as the rate of flow remains fairly high, the stream will carry a load of soil eroded from the more elevated regions. As the rate of flow decreases, the size of the particles it carries will decrease, until finally only silt will be held in suspension when the flow becomes sluggish. When the stream, which by now has perhaps developed into a river, empties into the ocean, the final precipitation of the finely divided particles of earth will occur, forming deltas which may be of vast extent.

If it were possible to watch long enough, a single location along a stream could be observed and the process of change from a swift stream to a sluggish one could be recorded. But this would require many centuries or even thousands of years. Fortunately for the ecologist, however, this succession may be observed in a short period of time just as we can observe the various communities involved in the succession of lakes. In the latter case, we look at different lakes in varying stages of development, or we study the zonation of littoral communities. With streams one merely needs to travel the length of any one to see the various seral stages in its succession. Thus the headwaters of the stream possess the aspects of a young stream, the larger and slower regions an intermediate stage; and finally, where the stream becomes a deep river, the characteristics of a mature stream are present. Therefore, as a stream accomplishes base leveling, organisms once able to live only in the lower parts of the stream are able to move upstream into the tributaries (Adams, 1901). The physiographic changes occurring with base leveling of streams thus allow a special type of succession to occur (Shelford, 1911).

Physical Conditions in Swift Streams

In the headwaters, various physical factors which are interrelated with the swiftness of the current are important to the life of the stream. There is a tendency toward large fluctuations in volume and flow of water from season to season. During the spring especially, small streams are unusually swollen. During the summer, these same streams may become almost completely dry. Such extreme variations require special means for organisms to remain in place and to survive under widely different conditions. The swift current can carry away small particles of rock so that, in general, the swifter the stream, the larger the rocks remaining in its bed (Fig. 7-27*a*, *b*). The large rocks form places of shelter and attachment for organisms, although even these big boulders may be moved during high water.

The bottom is normally composed of rocks and pebbles of various sizes, and occasionally, as on the inside of a bend, of gravel or sand. The water of swift streams reflects this bottom type and is clear, except during flood stage. There are,

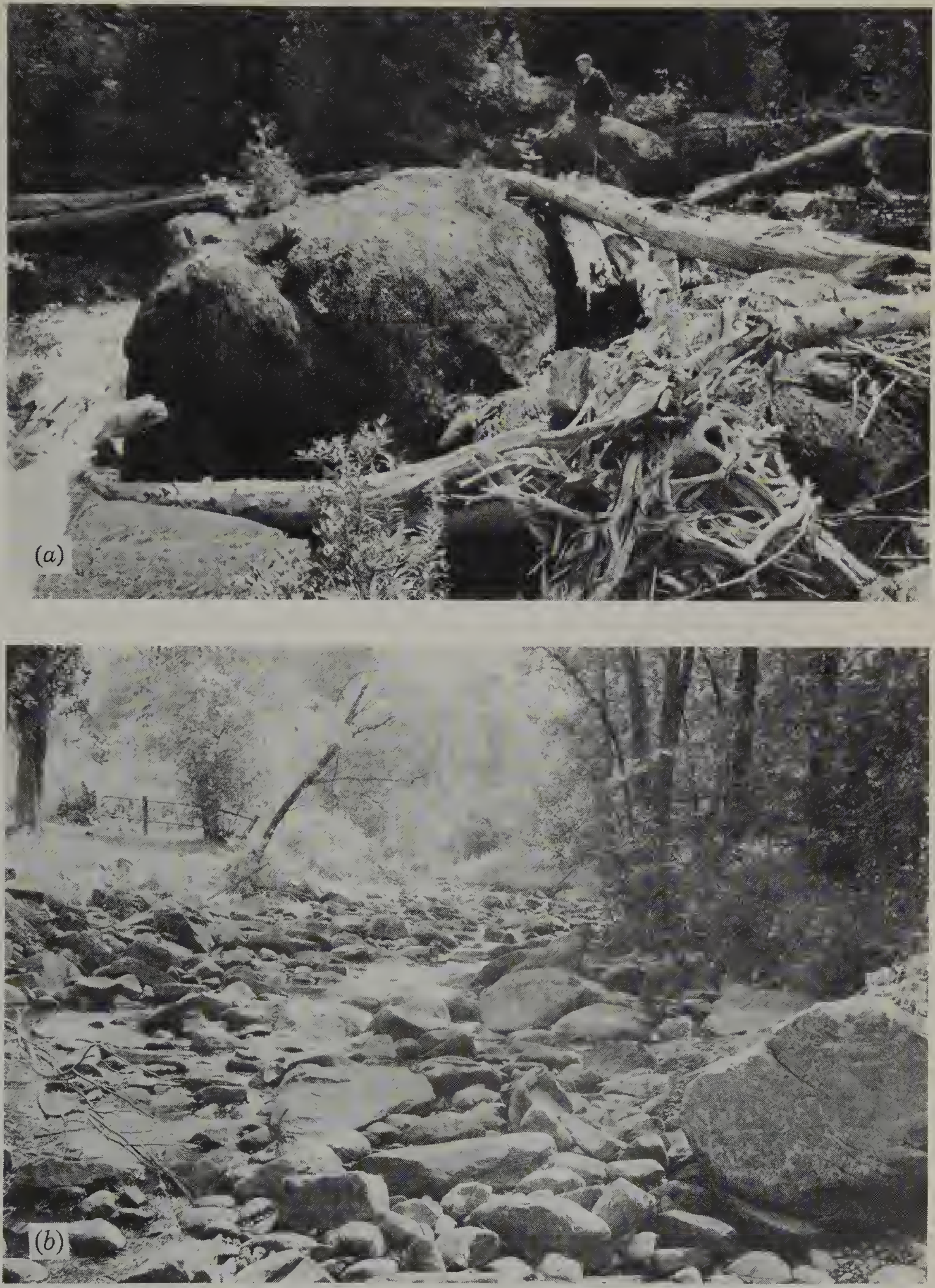

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Fig. 7-27 Effect of swiftness of current on size of rocks in stream bed:
(*a*) Huge boulders in a mountain stream.
(*b*) Large rocks and boulders in a swift stream.

in other words, relatively small amounts of finely divided soil particles or organic matter in the water. In occasional pools, however, several conditions are different from those found in the riffles. Among others, current may be reduced, and therefore deposition of fine particles may occur, which thus changes the bottom type in these locations to mud or silt.

Although the current flows swiftly in headwaters, it is usually relatively shallow, with only occasional deep pools. These conditions, too, affect the biota. The shallowness of the water permits excellent aeration (Fig. 7-28), but it also means that the temperatures here may vary more or less with the temperature of the atmosphere. The only exception to this will be when the stream is covered with ice, at which time the temperature of the water is stabilized near the freezing point. Since the amount of carbon dioxide and oxygen that may be dissolved in water is directly affected by the temperature, it follows that there is a continual variation in the amounts of these gases in the water, except during the period when the stream is covered with ice. However, oxygen content of swift streams, because of constant aeration and cool temperatures, is usually high. Some stability of the water temperature is afforded by trees and shrubs that usually line

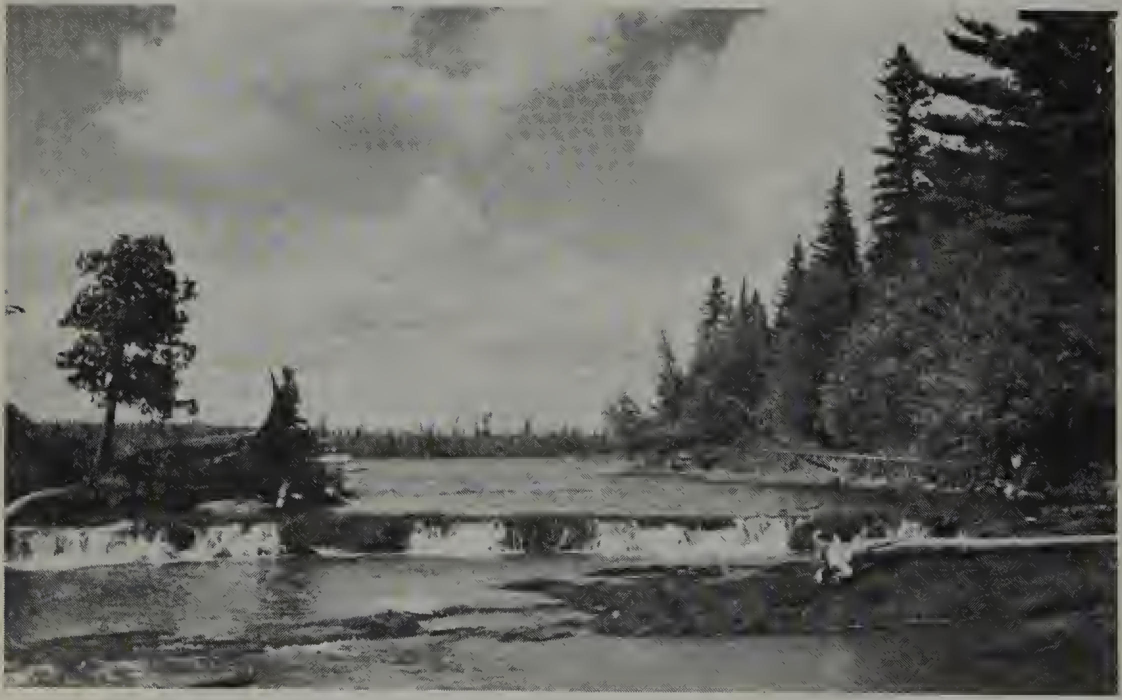

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Fig. 7-28 A shallow, swift stream permits excellent aeration of the water.

the banks of small, swift streams. Their shade prevents excessive warming by the sun, which would otherwise quickly heat the shallow water.

Adaptation for Swift-water Life

Because life in the swift streams is precarious or impossible for many organisms, the inhabitants of this environment are like the pioneers in other successions: they are able to endure severe environmental conditions. Various attributes of swift-water organisms enable them to survive the rigors of their habitat. They may have special hold-fast mechanisms, or a streamlined shape, special respiratory apparatus, or unique food-getting devices. In addition, many of the smaller forms must be able to reproduce rapidly, for the loss of life during the high-water period is great.

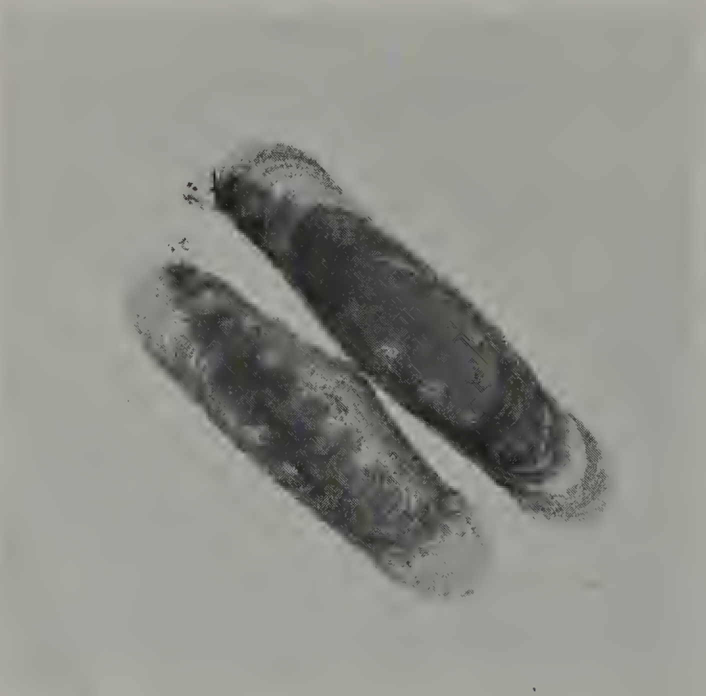
Permanently rooted aquatic plants are practically nonexistent in swift streams. Only in pools may a few such plants be found. The swiftness of the current makes attachment difficult, and the fluctuations in water level are also prohibitive to their existence. Instead, filamentous algae such as *Cladophora* and *Ulothrix* cling to the rocks by means of holdfasts; among their filaments are smaller algae such as diatoms and desmids. These minute plants are the basic food for all animals living in such water.

A group of plants found in streams which needs further study is fungi. Cooke (1961) found more than 90 species of soil fungi growing in a stream, and points out that fungi may have an important function in stream purification by aiding in reduction of organic waste materials.

The animals of this habitat are adapted either to swim against the current for short periods as they dart from rock to rock, or to cling by some means in open water or behind or under rocks. Their body forms frequently reflect the environmental conditions of their lives, in being streamlined or otherwise adapted for the least resistance to the friction of the water. One of the more abundant insects of this community is the black fly. Its larvae are frequently so numerous as to cover large areas of the rocks, giving them a velvety black appearance. These larvae are able to maintain their positions in fast water by means of an adhesive disk at their posterior ends. If they care to move, or if they are swept loose, they spin a silken lifeline from their mouths to prevent being carried downstream. Midge larvae are also common in swift water, as is the water penny—the larva of a small beetle, which is so flattened that it is able to cling, as does a limpet, to the undersurface of rocks.

Since traveling in fast water is perilous, it is not surprising that some swift-water animals have come to exist by means of devices which enable them to catch their food as it goes by. An example of such an animal is the larva of *Hydropsyche,* a net-spinning caddis fly. Its silken basket is arranged to catch plankton drifting with the current. Other caddis flies live in cases which they have fashioned from bits of stones or debris (Fig. 7-29); they also feed on plankton. Certain snails, limpets, and crayfish are among the larger invertebrates of this community, while flatworms and larvae of such insects as May flies, stone flies, dragonflies, and damsel flies also make the stony habitat of the bottom their home.

Since plant food is largely restricted to small algae and phytoplankton, it is not surprising that detritus feeders and predators are common among the animals present. Thus Chapman and Demory (1963) found that algae feeders included certain stone flies, caddis flies, and beetle larvae.



Minnie B. Scotland

Fig. 7-29 Two caddis flies, *Agraylea multipunctata,* in their cases. Larvae of this order are aquatic, and many are adapted to life in swift water.

Detritus feeders were found among some species of immature May flies, stone flies, caddis flies, and flies. Certain stone fly and caddis fly nymphs were found to be carnivores. Some, like May fly nymphs may be algae feeders one season, detritus feeders another.

A few species of fish are able to survive the rigors of the swift-water community. Trout and such smaller fishes as the daces, shiners, and minnows live in this habitat. These fishes usually spend most of their time behind rocks and dart for the shelter of other rocks when they move, not maintaining a position in the current for any length of time. Several swift-water forms like the long-nosed dace have terete bodies, while the stone roller minnow is rather unusual in having a lower lip specially reinforced with cartilage, which it uses for scraping algae off rocks. In some of these species the swim bladder is reduced or nonfunctional, enabling the organisms to stay on the bottom of the stream.

In a study of Kentucky streams, Kuehne (1962) found that certain fish were characteristic of different-sized streams and proposed a scheme of classification that should help in comparing studies of streams throughout the country. Thus, in the headwaters (first-order streams) he studied, creek chubs were the only fish present. In second-order streams (formed by the union of two first-order streams) creek chubs dominated but now arrow darters and stone rollers were common. Third-order streams (formed by the union of two second-order streams) were dominated by these same fish, but other species also appeared. In fourth-order streams (formed by the union of two third-order streams) creek chubs and arrow darters became uncommon or rare, and seven other species appeared for the first time. Similar differences in the benthos of streams of different sizes was found by Gersbacher (1937). In this study of Illinois streams, headwater invertebrates were dominated by *Chironomus* (a bloodworm), large creeks or small rivers by *Musculium* (a clam) and *Lampsilis* (a snail), and large rivers by *Hexagenia* (a May fly), *Chironomus*, and *Viviparus* (a snail).

Higher vertebrates are not numerous in swift streams. Worthy of mention are a few salamanders which may be found under the rocks in swift water. These include the dusky salamander (*Desmognathus fuscus*), purple salamander (*Gyrinophilus porphyriticus*), and two-lined salamander (*Eurycea bislineata*). The beautifully adapted water shrew (*Sorex* *palustris*) is an excellent swimmer and has fringes of hair along its feet which permit it to walk upon the surface of the water. It is found along small swift streams in wooded areas. Mink, raccoons, and other predators may feed along the edge of the stream but are not properly part of the stream community itself, in spite of their undoubtedly important effect upon it.

Although a relatively small number of species of organisms are able to live in the swift-stream community, the number of individuals may be very great. Thousands of invertebrates, of several phyla, can exist on a single rock, not to mention the bacteria and protozoa and other phytoplankton and zooplankton which exist around it. A single sweep of a seine may bring up a hundred small fishes. What is lacking in variation is made up for in numbers.

In swift streams, both flooding and droughts may kill whole populations. In floods, animals are killed as they are dashed about or are left stranded as flood waters recede. In an intermittent stream in Arizona, John (1964) found that the young of the year of the only species of fish present (*Rhinichthys osculus*) were especially vulnerable to flash floods, but older fish were most affected by the starvation occurring in overcrowded pools that remained during droughts.

Repopulation of small streams after floods or droughts is relatively rapid. Some parts of these streams may not be as severely affected by floods as others because of topography and may thus serve as population reservoirs. Adult insects may fly in or move up from downstream. In a study of drought in the headwaters of an Illinois stream, Larimore et al. (1959) found that in only two weeks 21 of 29 regularly occurring species of fish had reoccupied the stream as they moved up from downstream populations.

Pools are also important in providing refuge for organisms during droughts, from which repopulation may occur. Pools further act as nesting and nursery grounds for some fish and provide conditions suitable for survival of larger fish (Lagler et al., 1962). Populations of riffles are greater in numbers than those in pools while the stream is flowing, but other than this, the difference in fauna of riffles and pools in one section of the stream is not great (Stehr and Branson, 1938). As Kuehne (1962) points out, a greater difference occurs between the populations of upstream and downstream riffles. Riffles may act as boundaries for local populations of fish in the deeper sections of the stream, at least for fish which exhibit territorialism, such as certain suckers, sunfish, and bass (Gerking, 1953). Riffles are also important as spawning grounds where some species of fish (certain trout, darters, minnows, suckers) may bury eggs and as a habitat for aquatic insect larvae and other invertebrates such as crayfish.

Physical Conditions of Slow Streams

Where the elevation gradient is less, the stream will be slower. Usually such a slow stream will be deep and muddy-bottomed, located in a wide valley carved out by the stream itself (Fig. 7-30). The rate of flow and depth may still vary and be exceptionally great in rainy seasons. Flooding into its floodplain is a common occurrence. The lack of a strong current has its effect on other physical factors and ultimately on the type of community living in this habitat. Since it takes a strong current to move large rocks, few will be found, and silt or sand may form the bottom sediment. Near the shore and in shallow water where rooted vegetation grows, there may be accumulations of organic matter, which combine with the silt to form deep muck. Water temperature in slow streams is usually higher than that of swift streams, although deep-bottom waters may be cool. There is less chance for

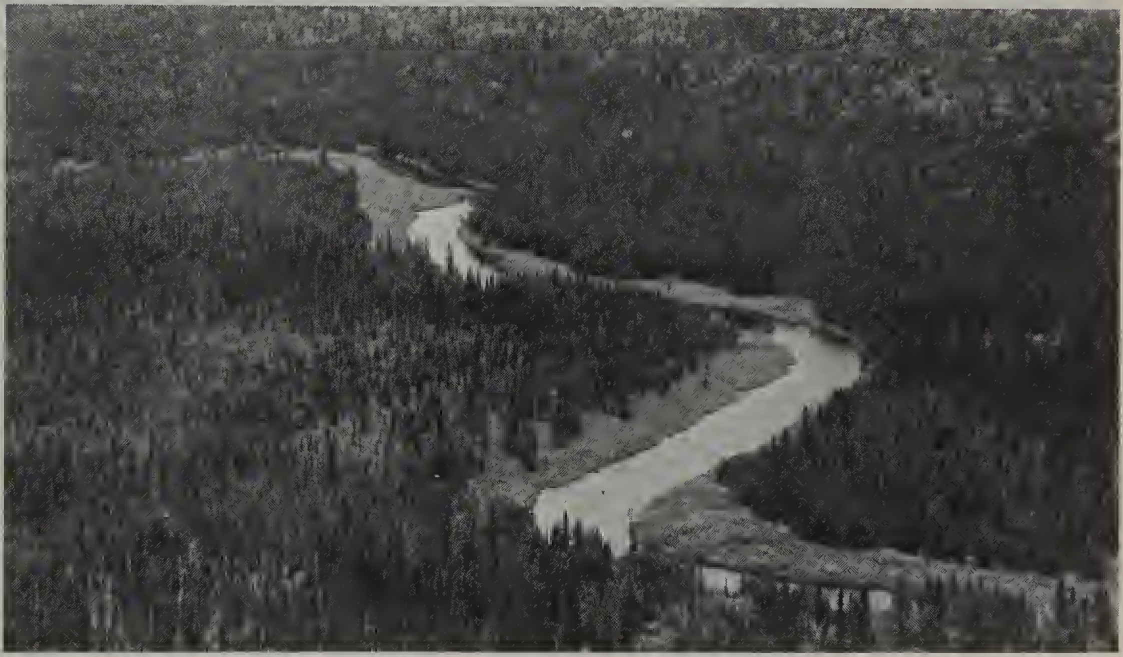


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Fig. 7-30 A slow meandering stream in a wide valley. Piscataquis County, Maine.

aeration of the water here than in a fast stream, so that oxygen content will be lower and carbon dioxide content higher. The water will usually be turbid. In a study of the lower Missouri River, in fact, Berner (1951) found that turbidity of the water was an all-important feature of the river, affecting almost every other characteristic.

The Life of Slow Streams

Since in still water there is no problem of maintaining position, plants are nearly always to be found along the shores of slow streams, and sometimes rooted aquatic plants such as *Potamogeton* may extend out into the center of a shallow stream. In backwaters, and sometimes along the shores, there may be the same zonation of communities found in lakes (Fig. 7-31). Plankton is also different in the slow stream. In addition to the desmids, diatoms, and other small forms of algae found in swift streams, protozoa and rotifers abound. In some rivers, plankton increases in numbers as the stream

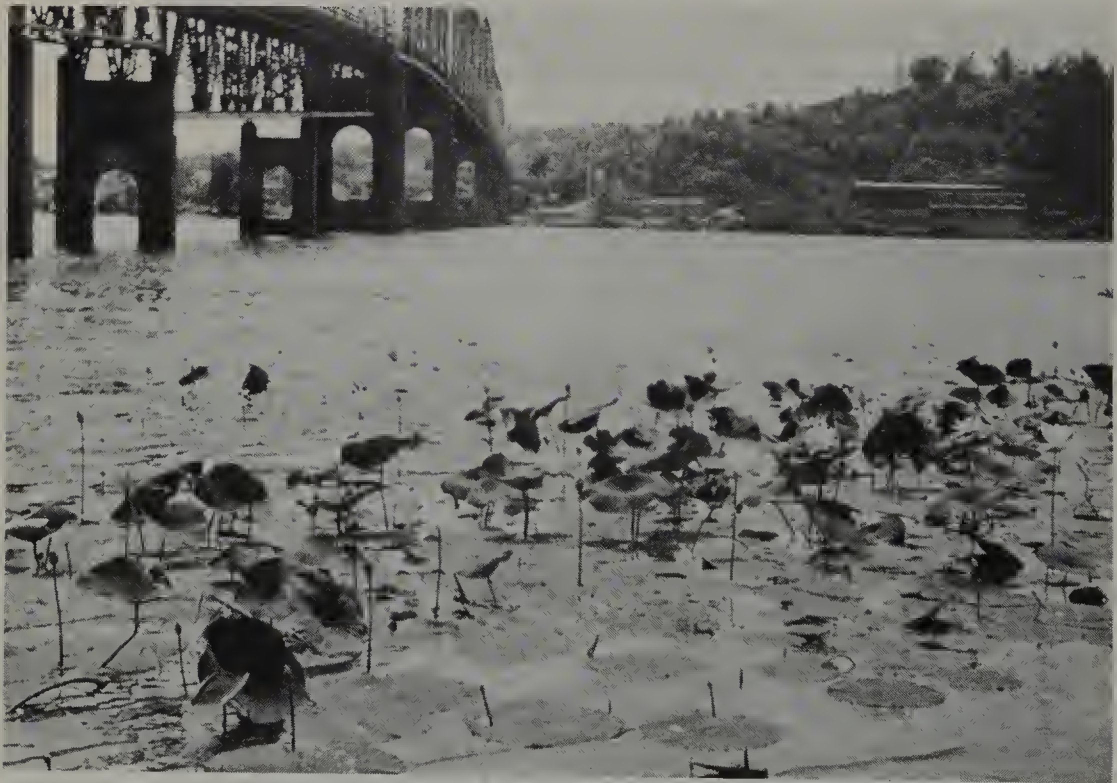

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Fig. 7-31 Aquatic vegetation zones in a backwater of a river show marked similarities to the same communities in lakes (cf. Fig. 7-14). Mississippi River at Hannibal, Missouri.

progresses from its headwaters, reaches a maximum, and then declines near the mouth of the river (Welch, 1952). Part of the decline may be due to the effects of the rooted aquatic vegetation, which acts as a strainer to prevent the further movement of the plankton downstream.

In slow streams as well as swift, there is usually a considerable population of drifting organisms. Thus Berner (1951) found an average of 0.07 pounds per surface acre in the relatively unproductive Missouri. Waters (1961) believes that a measurement of drift organisms may be used as an index of productivity of stream benthos, since such organisms represent the surplus of populations that have lost out in competition for space and other requirements.

Various factors may affect plankton productivity in large streams. In the lower Missouri River, plankton populations are very low, mainly as a result of the high turbidity (Berner, 1951). Also important is the low concentration of oxygen (less than 50 per cent saturation in midsummer). In the Sacramento River, California, plankton increases progressively downstream. In this case, water temperature was the most important factor affecting plankton populations, although current and oxygen concentrations were also important (Greenberg, 1964).

Animals of the slow stream are more varied than is the case in swift water, and include greater numbers of large species. Yet the bottom fauna may not be more numerous; for without stones, suitable dwelling places, except for burrowing animals, are lacking. Snails, clams, bryozoans, amphipods, leeches, crayfish, and earthworms may be included in the fauna. Many insect larvae and adults, similar to those of littoral communities of lakes and ponds, will be present. Vertebrates are more plentiful as well as more varied. Usually fish species which occur in fast waters are not found in slow streams, perhaps because of their oxygen or temperature requirements. Some require particular conditions for parts of their life cycle, such as a certain type of bottom for spawning. Silt covering the bottom rubble may prevent successful breeding by certain fast-water forms. In the larger rivers, gill-breathing salamanders like the mud puppy, *Necturus*, and large turtles like the snapper, *Chelydra*, are frequently present.

The Upstream Movement of Succession

As the headwaters of a stream wear the hills down, more and more of the stream will have a slow current, and so succession moves upstream. The slow-water community invades and replaces the swift-water community. If we travel the length of a stream, we may observe a gradual change in biota as the shift from slow to swift water takes place. There will be irregularities in the transition, for rapids will be interrupted by pools, and these pools may possess some species belonging to the slow-water community. Furthermore, the current is not uniform across a stream, nor from the surface to the bottom, and these variations will produce deviations in the community. In general, however, the sere is clearly recognizable and demonstrates a kind of succession.

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chapter 8

The marine environment

The study of the oceans is called oceanography. This science is a very broad one and consists of several major divisions: physical oceanography, which deals with currents, waves, tides, density, conductivity, transparency, and other properties of sea water; geological oceanography, which includes the study of the formation of the ocean floor, sedimentation, bottom topography, and erosion; chemical oceanography, which is concerned with the constituents of the salts in the oceans, the elements, and organic and inorganic compounds in the oceans; and biological oceanography, which deals with all aspects of life in the sea. Very often studies in one of these divisions require knowledge of the others, especially in geological and biological oceanography. Some studies are restricted primarily to the open oceans, while others are concerned primarily with coastal waters. On the other hand, all aspects of the oceans may be of significance to any other one.

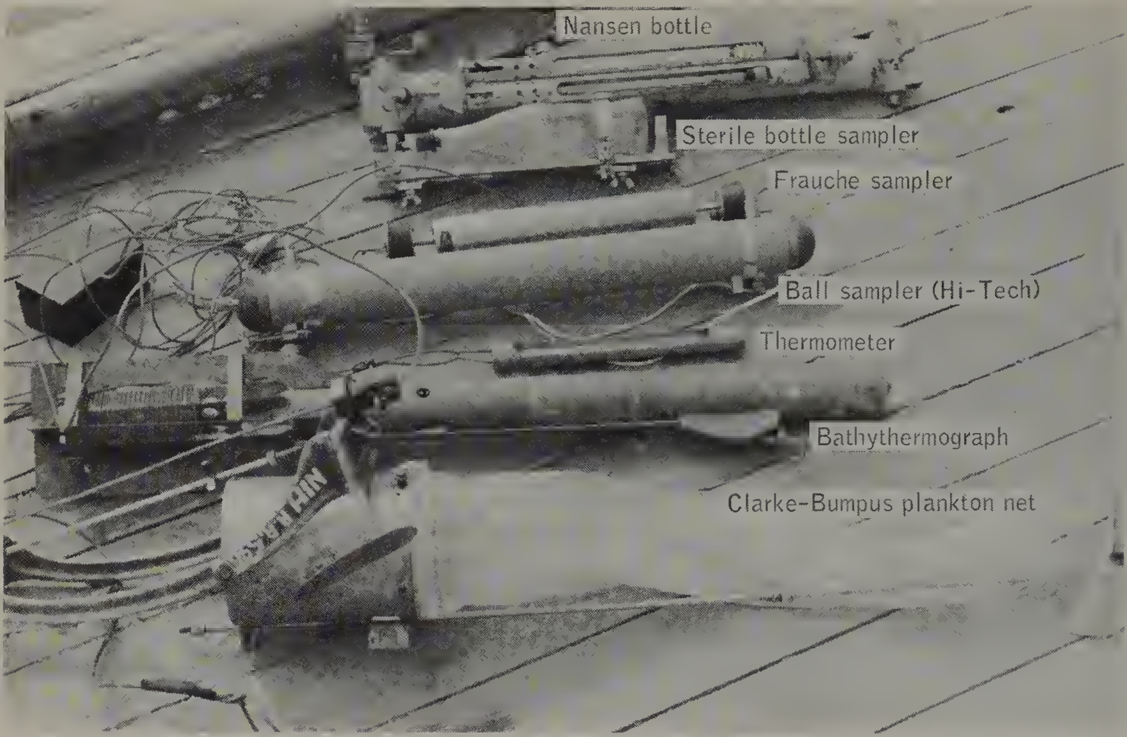
The study of the open oceans has, until recent times, been

Beneath the waves there are many dominions yet to be visited and kingdoms to be discovered, and he who venturously brings up from the abyss enough of their inhabitants to display the physiognomy of the country, will taste that cup of delight, the sweetness of whose draught only those who have made a discovery know.

Edward Forbes, "Natural History of European Seas," 1859

rather limited. Most of the biological work was taxonomic, a necessary first step to find out what organisms exist in the sea, and where. More recently there has been a surge in oceanographic work, some of it being carried on in land-based laboratories, and some of it on board oceanographic vessels.

Many studies can be made only on the oceans. For example, the research dealing with ocean currents, their paths, temperatures, salinity, and other properties must be made at sea. Organisms brought up from the ocean depths must often be studied in the living condition on the spot. Research conducted under these circumstances is expensive, and this fact is probably one of the reasons for the paucity of our knowledge of the oceans, for only governments and modern-day foundations are wealthy enough to support research requiring oceanic vessels. Dupree (1959) gives an interesting account of the difficulties of obtaining financial support for oceanic expeditions a century ago. Today, governments are more



William E. Werner, Jr.

(*a*) Sampling devices (from top to bottom): a Nansen bottle with reversing thermometer, a sterile bottle sampler, a Frauche sampler, a Hi-Tech Ball sampler, a thermometer, a bathythermograph which makes continuous recordings of temperature as it is lowered, and a Clark-Bumpus plankton net.

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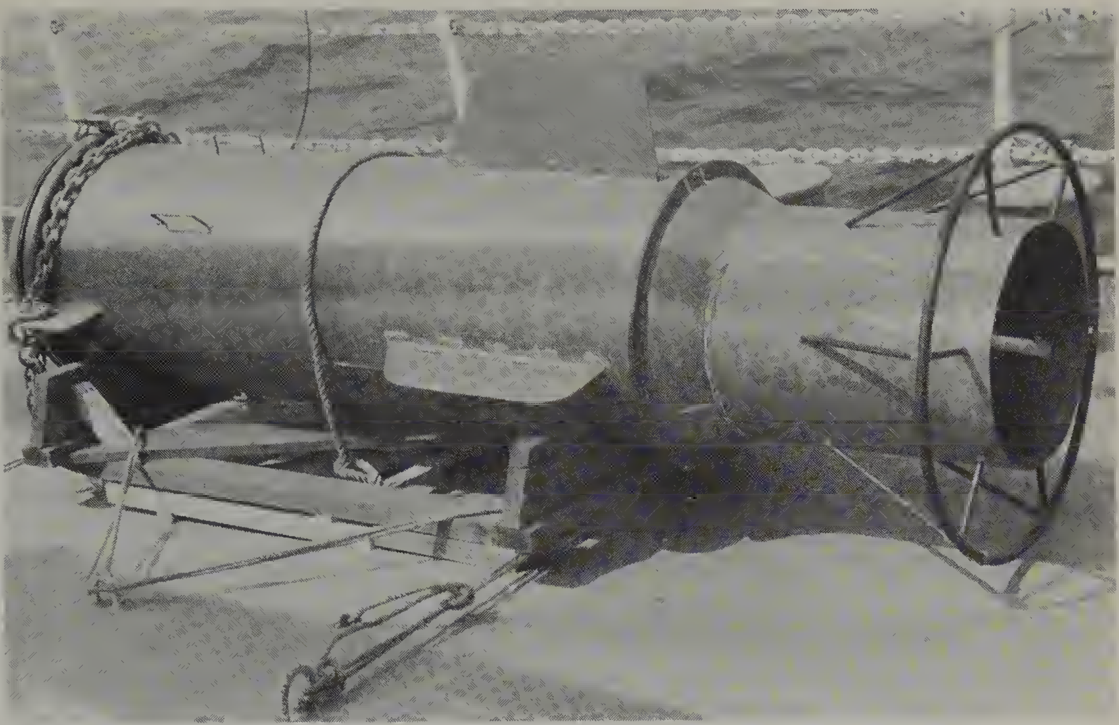
(*b*) A Van Veen grab, capable of taking a bottom sample of approximately ⅕ square meter.



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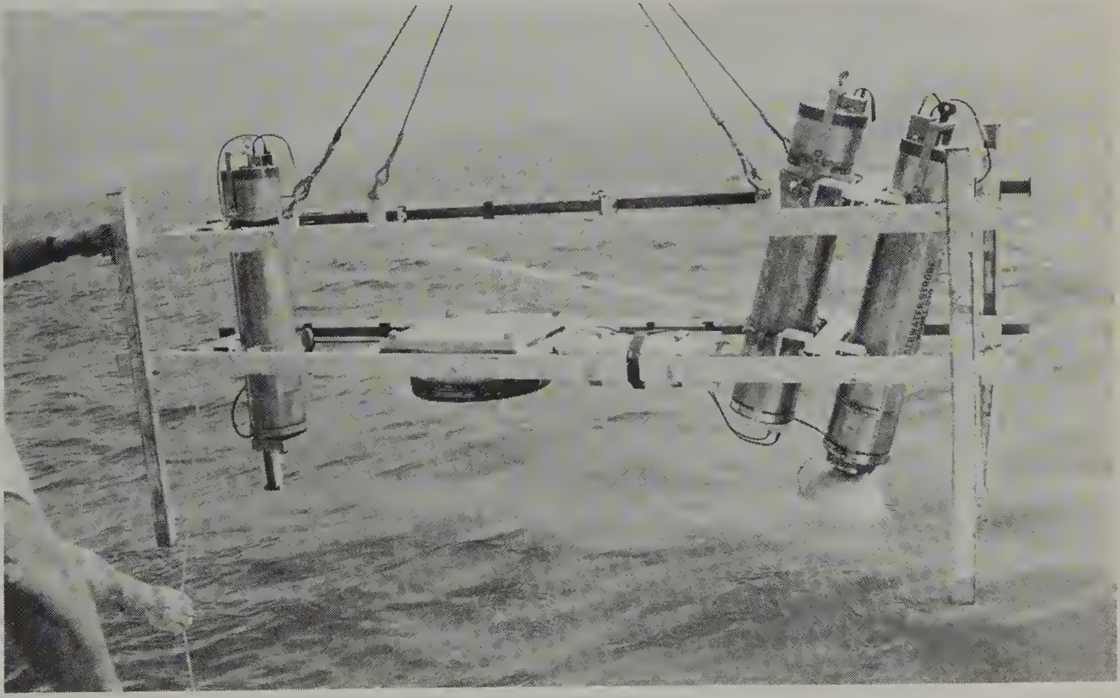
(*c*) The housing for a large high-speed plankton net.



William E. Werner, Jr.

(*d*) An Edgerton camera for photographing the bottom. A strobe light flashes and a picture is taken simultaneously at 12-second intervals. A "pinger" on the device allows the operator to determine when the camera is near the bottom.

Fig. 8-1 Some oceanographic equipment.

interested in supporting oceanic research since its economic importance has been demonstrated.

Another reason for the more recent surge of research in oceanography is the development of suitable equipment and techniques. Magellan used a cannon ball on a rope in an unsuccessful attempt to plumb the depth of the ocean, whereas today research vessels use electronic sonar devices which make a continuous record of the depth of the ocean under the ship. Expeditions until the late nineteenth century used rope to lower dredges or other sampling devices. Even the famous Challenger Expedition of 1873–1876 used rope, although wire was tried. Today, steel cables and power-driven winches lower and raise water-sample bottles, plankton nets, trawls, dredges, coring devices, and photographic equipment (Fig. 8-1).

The vastness of the oceans is another reason for the spottiness of our knowledge of the sea. The surface area of the oceans is over 126 million square miles or approximately 71 per cent of the earth's surface. Its depths (such as the Mindinao Trench, 37,782 feet) are greater than the elevations of the highest mountains, and the average depth is approximately 5 times the average height of land. One of the difficulties posed by oceanic exploration, then, is the vastness of the seas compared with the puny-sized samples oceanographers are able to take. Collecting devices cannot be large because of the size and weight of the cable that would be required to lower big samplers to great depths. Even with modern power winches, it may take several hours to lower a net to the bottom and several more to raise it. Currents and movements of the vessel may foul the gear, so that nets may come up empty or filled with unwanted bottom debris. Diving suits allow a man to descend to a maximum of about 535 feet. The bathyscaph *Trieste* has descended to over 35,000 feet (Piccard, 1960), and from it one may observe organisms and photograph them, make temperature and current recordings, and even pick up some objects. However, our knowledge of life on the ocean bottoms and at great depths is still meager. For example, it was not until the Galathea Expedition of 1950–1952 that it was ascertained that there was abundant life at great depths.

One difficulty of ocean studies in the past has been that one vessel working in one part of the ocean could obtain data from only a very limited area of the ocean at any one time. Recently, the Indian Ocean Expedition of 1961–1963 was conducted, in which 40 ships of 25 nations participated. Meanwhile, the equatorial Atlantic Ocean is being studied by vessels of eight nations in projects called Equilant I and II. The data from all ships are processed and sent to all participating nations. From such research, man is gradually piecing together a total picture of the physical, chemical, geological, and biological conditions of the oceans.

CLASSIFICATION OF MARINE ENVIRONMENTS AND COMMUNITIES

The classification of marine environments proposed by Hedgpeth (1957*b*) has gained considerable acceptance (Fig. 8-2). According to this scheme, there are two major environments in the sea, *benthic* (bottom) and *pelagic* (open sea).

Benthic Environments

The uppermost of the benthic habitats is the supralittoral zone, which is the beach down to the edge of the sea. Where there are tides, the lower boundary of the supralittoral is the

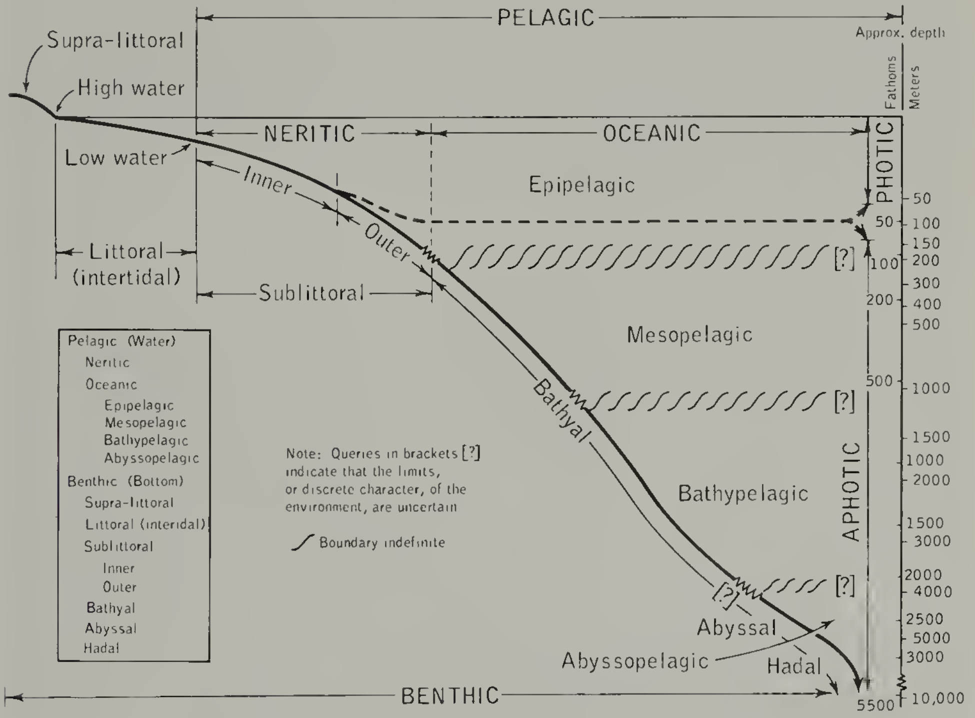


Fig. 8-2 A classification of marine environments. From Hedgpeth, J. W. 1957. In "Treatise of Limnology and Paleoecology, Vol. I, Ecology." *Geol. Soc. Am. Mem.* 67. New York, pp. 17–27.

high-tide mark. The littoral zone is the area between upper and lower tide levels and is therefore called the intertidal level by some. It is the margin of the sea. The sublittoral zone extends from the lower limit of the littoral to the edge of the continental shelf. The sublittoral is divided into the inner and outer sublittoral. The inner sublittoral is distinguished from the outer by the presence of attached algae in the former, the latter being too deep (50 to 200 meters) for effective photosynthesis. The *bathyal* zone occurs on the continental slope, where the bottom of the ocean descends rapidly from about 200 meters down to 3,000 or 4,000 meters. From this depth to approximately 6,000 meters is the *abyssal* region, in which the temperature is never above 4° Centigrade. In the great trenches of the ocean, where depths may be as great as 10,000 meters, the benthic zone is called *hadal*, since preliminary investigations indicate the fauna here is quite different from that of the abyssal zone (Hedgpeth, 1957*b*).

Pelagic Environments

The open sea above the benthic region is the other general environment and is known as the pelagic. The water over the continental shelf is that part of the pelagic known as the *neritic* zone, while the water over the continental slope and the greater ocean depths is called the *oceanic* zone. This in turn is divided into several subzones (*epipelagic, mesopelagic, bathypelagic*) according to various depths (Fig. 8-2).

Marine Communities

Agreement on a classification of marine communities is even more difficult than for a classification of environments. Several workers have used the term biome in describing littoral communities (Marshall, 1953; Shelford et al., 1935; and others). Allee et al. (1949) point out that according to certain criteria for biomes, there should be only two or possibly three marine biomes—benthic, pelagic, and possibly coral reefs, which they call biome-like. Kendeigh (1961) recognizes four biomes—pelagic, rocky shores, muddy and sandy beaches, and coral reefs and atolls. However, as Odum (1959) points out, benthic organisms are really a part of zonal communities, not major communities in themselves. In other words, pelagic and benthic organisms at a given depth are part of the same communities. Hedgpeth (1957*a*) points out that phenomena on land and in the oceans are not the same. Thus, although a kind of succession does occur (Hewatt, 1935; Reish, 1961; Shelford et al., 1935), it is quite different from terrestrial succession, and the concept of climax fits even less well. The factors determining the equilibrium of a marine community are primarily physical. It would seem best, at least at this stage of our knowledge of marine communities, if the terms applied to larger terrestrial communities, such as biomes and climax, are not applied to marine situations.

GENERAL FEATURES OF NORTH AMERICAN COASTS

Currents

The shores of the East coast exhibit several differences from those of the West coast, although there are of course many similarities too. Among the most important reasons for differences are the oceanic currents along each shore. The following description of surface water movements is extremely simplified and generalized, but for the purposes of this discussion brings out certain situations of significance. For detailed information on currents, see Sverdrup et al. (1942).

For various reasons, the general path of movement of the upper oceanic water on the East coast is toward the northeast. The warm current known as the Gulf Stream moves up from the Caribbean. A part of it, called the Florida Current, comes close to the shore off Florida. The Gulf Stream continues north along the coast and is met by the cold Labrador Current moving south from the arctic. These currents merge and move across the Atlantic as the North Atlantic Current. Eventually the current moves south along the western coast of Europe to the equator and then across the Atlantic as the North Equatorial Current, where it is warmed. It now moves once again up to the Caribbean. One part travels past the Yucatan Peninsula and into the Gulf of Mexico, then rejoins the remainder of the stream which has flowed to the east of the Caribbean. Water from the Southern Hemisphere also joins the stream in the Caribbean (Fig. 8-3*a*).

In the Pacific, the Kuroshio Current and its extension, the North Pacific Current, join the cold Subarctic Current below Alaska. Now called the California Current, it moves down the coast off Washington, Oregon, and California to Baja California, then turns west above the equator as the Pacific North Equatorial Current. Finally, the current, now warmed, turns

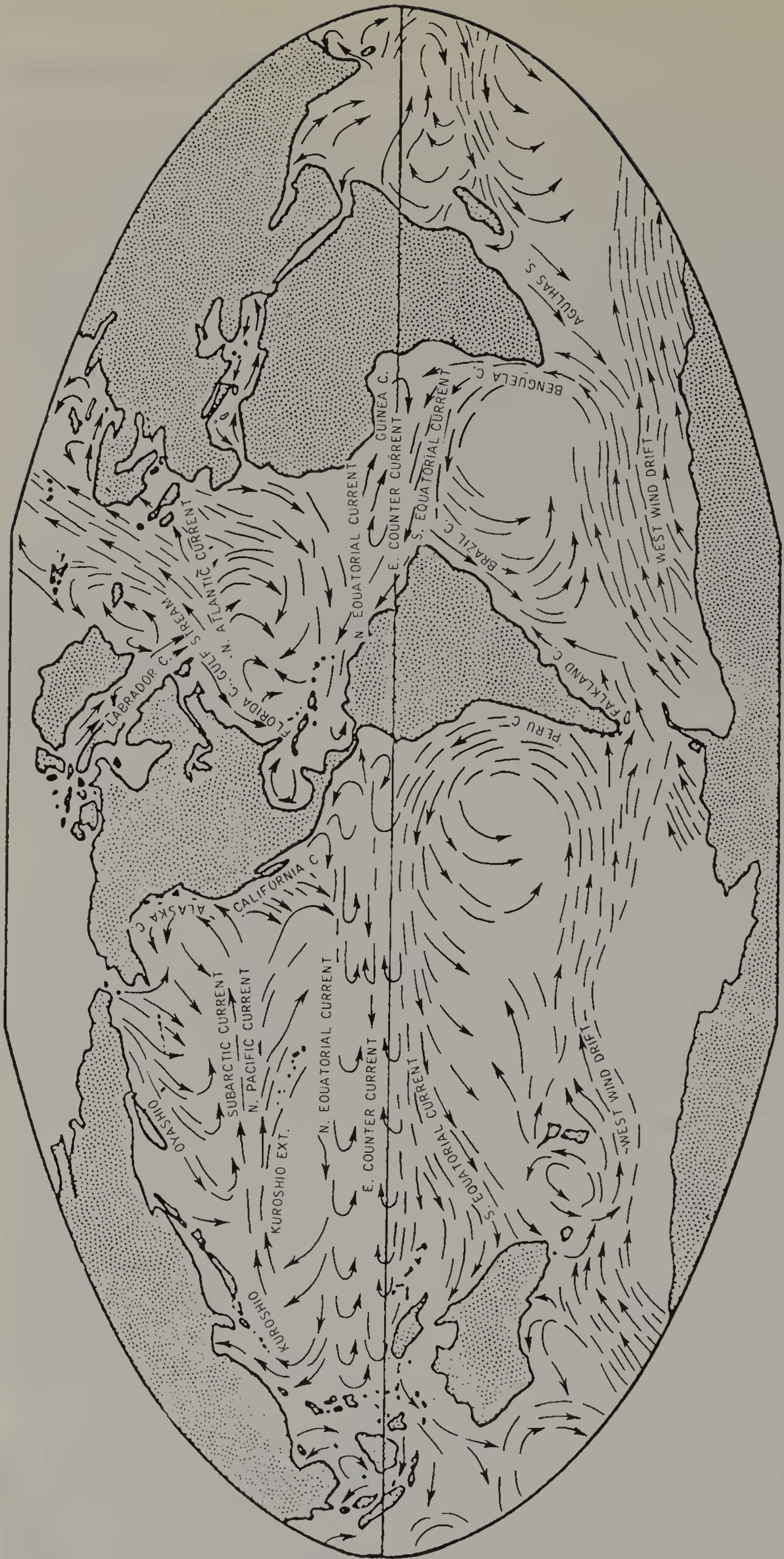
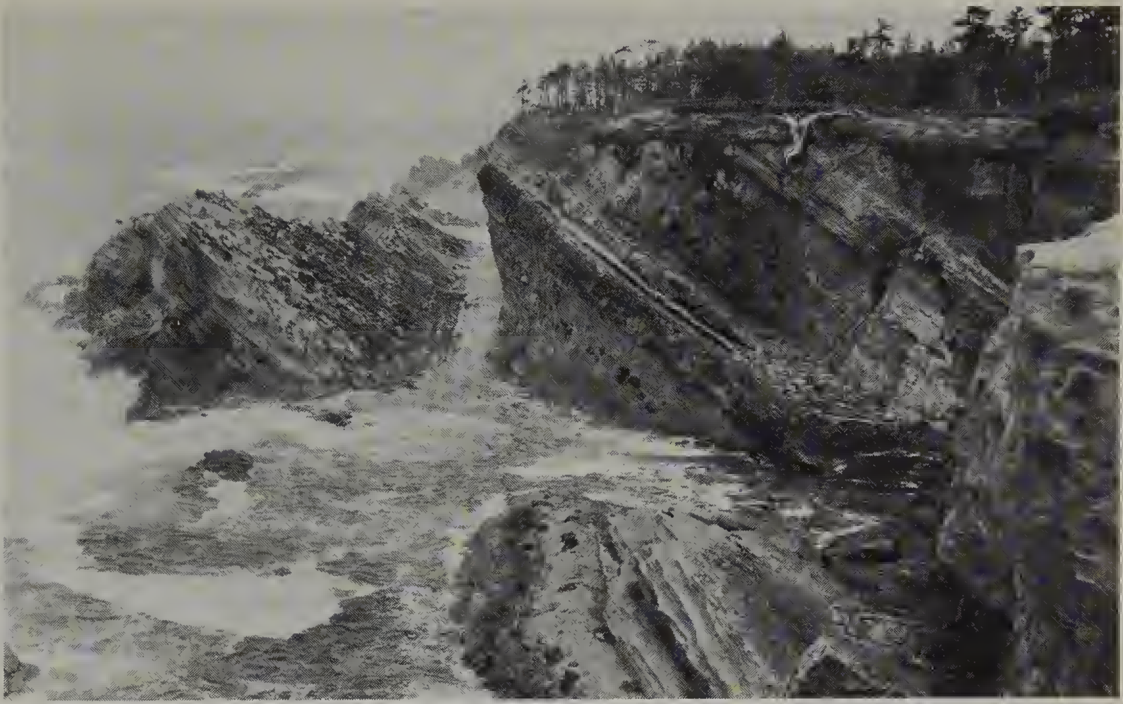


Fig. 8-3*a* Surface currents of the ocean in February-March. Data from Sverdrup et al., 1942, by permission of the publisher.



Allan G. Heath

Fig. 8-3*b* The surf along the Oregon coast. On exposed coasts, it is extremely dangerous to wade in the littoral zone because of the strength of the surf action and occasional high swells.

mostly north and flows on past Formosa and Japan, where it becomes once again the Kuroshio Current.

Thus on the East coast the currents flowing near the coast are warm, having come recently from equatorial locations, while the currents off the West coast are cold, having been chilled by arctic waters. Furthermore, upwelling of cold bottom waters along the Pacific coast tends to keep the coast cooler at much lower latitudes than one would ordinarily expect (Sverdrup et al., 1942).

Wave Shock

Another condition of importance to organisms is wave shock, which also differs on the two coasts. Because of the prevailing westerly direction of the winds and the absence of protecting coastal islands, the ground swells are much greater on the Pacific coast than on the Atlantic coast of North America (Fig. 8-3*b*). This results in much heavier surf and greater wave shock on the West coast than is generally found on the East coast (Ricketts and Calvin, 1952).

Dispersal Barriers

The union of the Labrador Current with the Gulf Stream occurs in part off Cape Cod, Massachusetts, creating a relatively sudden change in temperature of the ocean water. This presents a barrier across which many (but not all) marine species cannot pass, either from north to south or south to north, because they cannot tolerate the temperatures encountered beyond this point. Other dispersal barriers are said to exist at Newfoundland; Cape Hatteras, North Carolina; and Cape Kennedy, Florida, where there are critical changes in the ocean temperatures (Fig. 8-4). On the Pacific coast, temperature gradients are much more gradual, resulting in broad transitional zones rather than sharp dispersal barriers.

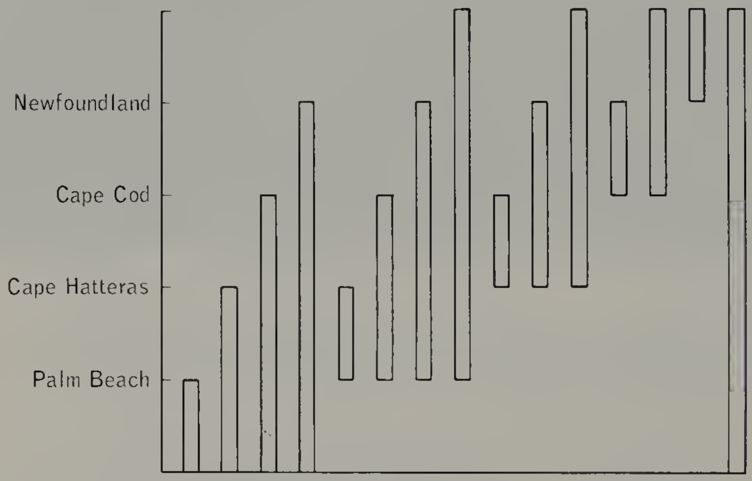


Fig. 8-4 Schematic representation of the components of the American coast biota, with reference to the important change-points of Newfoundland, Cape Cod, Cape Hatteras, and Palm Beach (Cape Kennedy). Fifteen possible ranges exist, of which fourteen are zonal and one is ubiquitous. From Hutchins, Louis W. 1947. The bases for temperature zonation in geographical distribution. *Ecol. Monographs,* 17:325–335.

It should be observed that the temperature tolerances which may limit a species' distribution may be more critical at one part of its life cycle than another. Hutchins (1947) devised a rule for the effects of temperature on the dispersal of various species, which states that the poleward limits for some species are determined by minimum temperatures. Some species reach a limit in poleward dispersal because the water is not warm enough in summer for breeding. Other species are stopped from further poleward dispersal because they reach a point where winter temperatures are too low for survival. Conversely, some species are limited equatorward by their inability to survive high summer temperatures, and others are limited in equatorward distribution by reaching the point where even winter temperatures are too warm for reproduction. Since these poleward and equatorward distribution requirements may be found in various combinations for any one species, there are four zonal types with respect to restriction of dispersal by temperature (Fig. 8-5*a*, *b*). Exceptions to this example of restriction of dispersal include situations in which the animal may be present in an area but does not complete its life cycle there. Also, each stage of the life cycle of an animal may be differently restricted in dispersal by temperature and other factors.

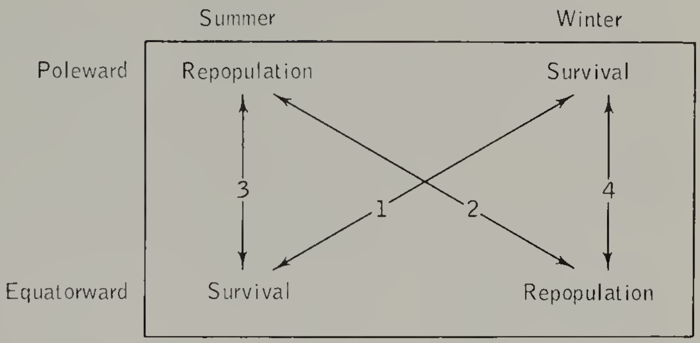


Fig. 8-5*a* Diagram of the four basic types of zonation, showing for each the season providing the critical poleward and equatorward conditions. The terms inside the box suggest the usual sort of relationships involved—i.e., survival tolerance of the most resistant stage, or the requirements for some phase of repopulation. From Hutchins, Louis W. 1947. The bases for temperature zonation in geographical distribution. *Ecol. Monographs,* 17:325–335.

Estuaries

Along the coasts there are, of course, the outlets of rivers and streams, and these create habitats called estuaries. An estuary may be defined as an inlet of the ocean where there is a mixture of fresh and salt water, or that part of a river emptying into the ocean which exhibits tidal phenomena. The water involved normally has a free connection with the ocean, allowing circulation of water and other substances. Examples of estuaries include the lower Hudson River, Chesapeake Bay, and the mouth of the Mississippi River, as well as the mouths

After some time (one or two months) the plankton populations decline, sometimes rather suddenly. Water at the surface has warmed rapidly, and there has been built up a large temperature gradient from the top to the bottom of the lake. The consequence of this is that the cooler, denser water of the bottom does not mix readily with the warm, light,

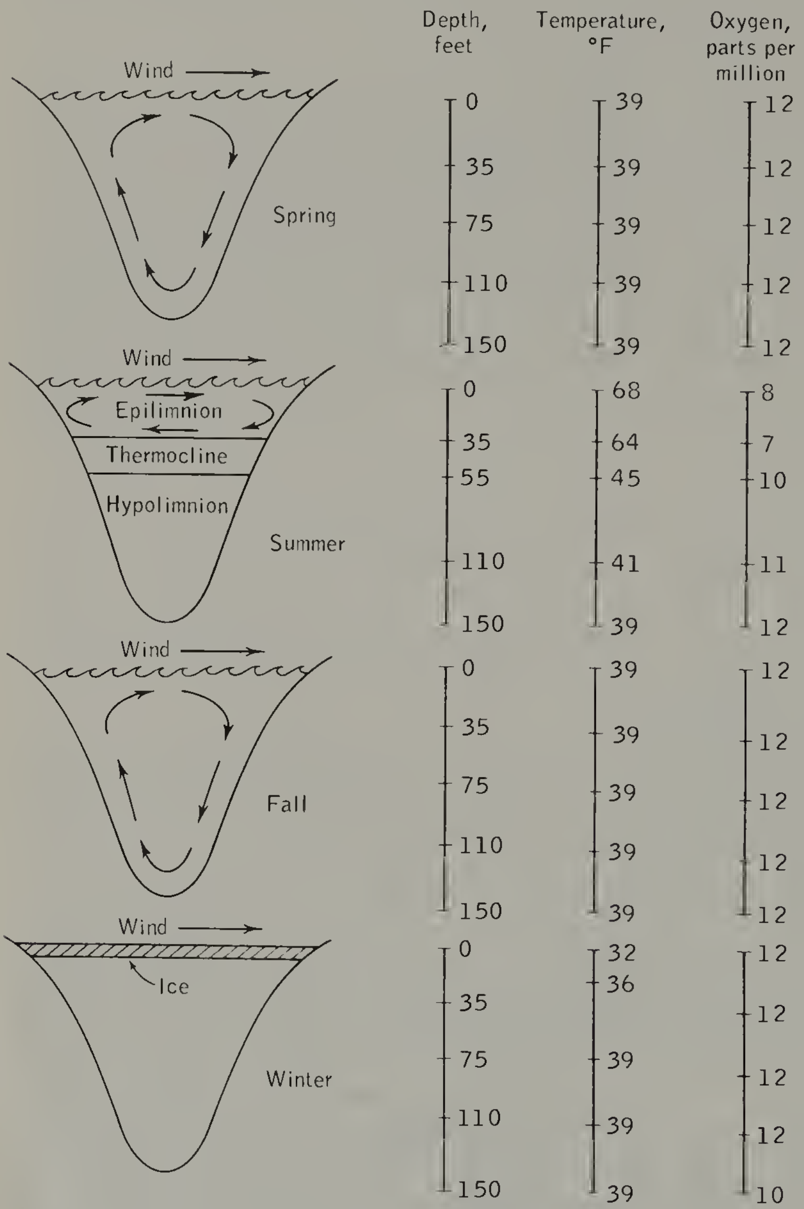


Fig. 7-7 Seasonal changes in a temperate oligotrophic lake. The temperatures and oxygen concentration at given depths are schematic. The exact temperature and oxygen concentration in any given lake at various depths will vary somewhat throughout each season, and each lake will exhibit variations from any other at any given time.

surface water. According to the thermal properties of water, the density of water increases rapidly from 4° Centigrade (to either higher or lower temperatures); a slight increase in temperature will decrease density (and hence resistance to mixing) rapidly. The upper layer of water is quickly warmed by the sun and consequently does not offer much resistance to mixing by the wind. However, as the temperatures of the water beneath this surface layer decrease even slightly with depth, the density and hence resistance to mixing increases rapidly. The sudden increase in density because of this small

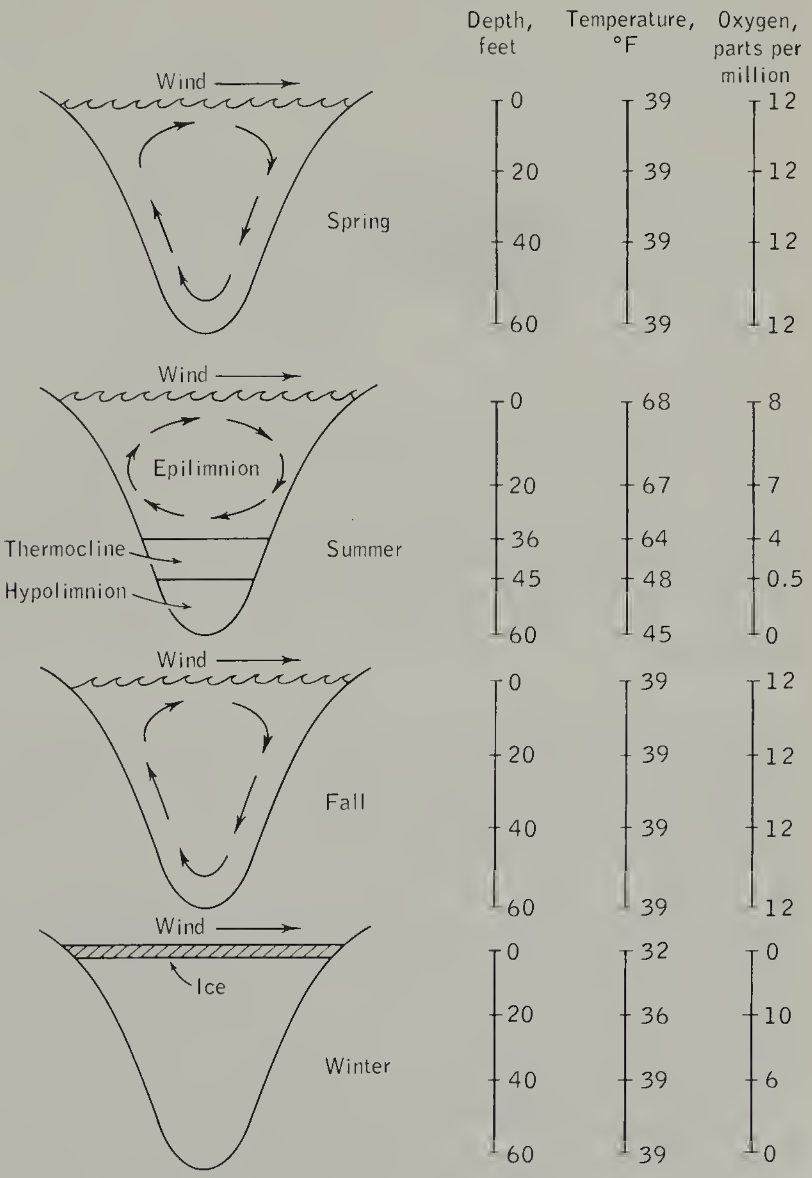


Fig. 7-8 Seasonal changes in a temperate eutrophic lake.

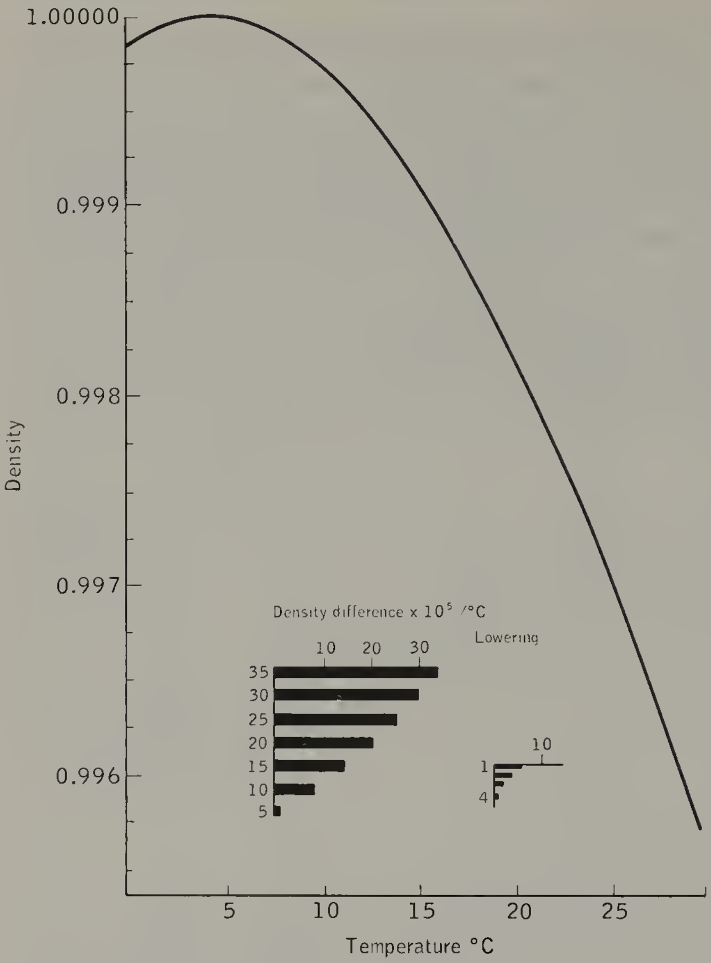


Fig. 7-9 Density as a function of temperature for distilled water. The density difference per degree Centigrade lowering is shown in the lower part of the figure for distilled water at various temperatures. From Vallentyne, J. R. 1957. The principles of modern limnology. *Am. Scientist,* 45:218–244.

difference in temperature tends to restrict circulation of water to the upper warm layer and thus makes it difficult for warming to progress downward. This leads to the establishment and maintenance of the thermocline and the consequent elimination of further mixing of the surface and bottom water. The water of the epilimnion continues to circulate, and the hypolimnion, although isolated, does not become depleted of oxygen. However, the epilimnion is now isolated from the bottom nutrients, and this may be one of the factors involved in the plankton decline in late summer (Fig. 7-10).

Although direct circulation of water by the wind is restricted to the epilimnion while the thermocline persists, there is some movement of water in the hypolimnion and thermocline. This movement is due to the effect of wind blowing in one direction, "piling up" epilimnion and thermocline water on the downwind (leeward) side of the lake, and depressing the hypolimnion under it. When the wind ceases, the water rushes back to the opposite side of the lake, and the hypolimnion is depressed on that side, meanwhile rising on the leeward side. It may take an hour to several days for one excursion of the wave across the lake and back, depending on the size of the lake. The wave causing alternate depres-

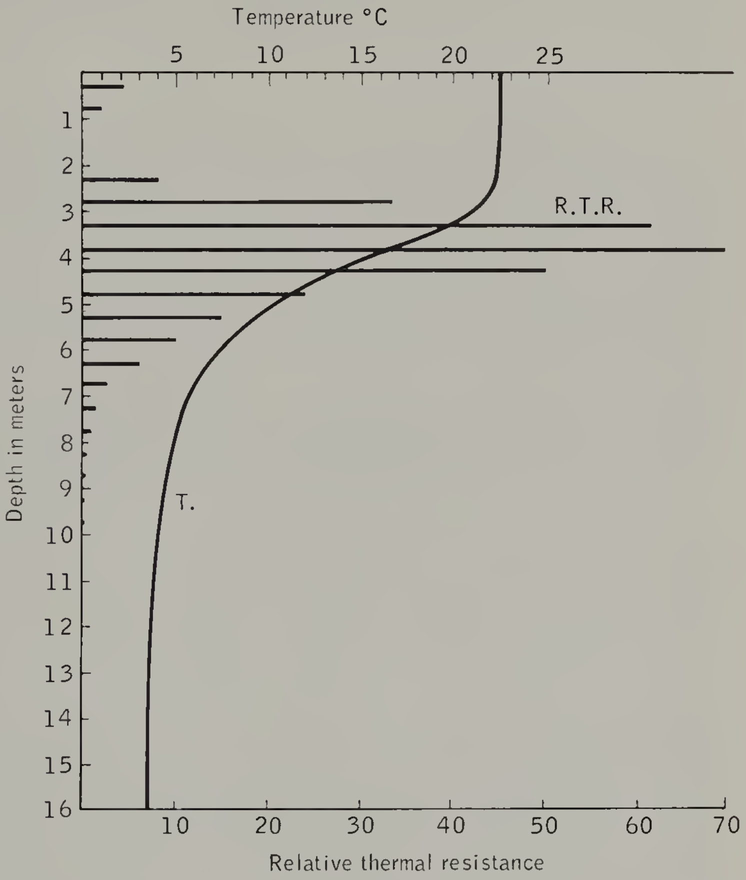


Fig. 7-10 A summer temperature profile (single line) and relative thermal resistance to mixing (bars) for Little Round Lake, Ontario. The relative thermal resistance (R.T.R.) to mixing is given for columns of water 0.5 meters long. One unit of R.T.R. = 8×10^{-5}, i.e., the density difference between water at 5° and 4° Centigrade. The R.T.R. of the lake water columns is expressed as the ratio of the density difference between water at the top and bottom of each column to the density difference between water at 5° and 4° Centigrade. From Vallentyne, J. R. 1957. The principles of modern limnology. *Am. Scientist,* 45:218–244.

sion and elevation of the hypolimnion continues oscillating back and forth across the lake about one or more nodes for some time (up to a week) after the wind has ceased. Although the surface of the water may be elevated only a fraction of an inch per mile of surface, the hypolimnion may be depressed a few yards per mile. There are many complications that may exist because of recurring winds, the size and bottom contour of the lake, the effects of the earth's rotation, and other conditions. Mortimer (1952) has studied these oscillating current systems (called *seiches*) extensively and points out that both the thermocline and hypolimnion are affected by such movements, which may alter the distribution of plankton and stir up an otherwise stagnant hypolimnion.

As fall approaches, the water on the surface and in the whole epilimnion cools. As it cools, the difference in density of the water of the epilimnion compared to that of the thermocline disappears. Strong fall winds are now able to circulate the water completely in the same manner as was done by the spring winds, and the thermocline (and hence thermal stratification) is destroyed. This fall overturn once again redistributes bottom materials, and frequently there are fall plankton blooms which decline as winter approaches.

With the coming of winter, the temperature of the whole lake is lowered. Large lakes may not freeze from shore to shore, but when freezing does occur, the water directly under the ice is the coldest, with the temperature increasing to 4° Centigrade at the bottom, the temperature at which water is heaviest (Fig. 7-9). In deep tropical lakes, the bottom temperatures may be only 20° to 25° Centigrade, since the bottom temperature cannot be lower than the average temperature of the air during the previous overturn (Vallentyne, 1957). Since oligotrophic lakes are fairly deep, the cold water holds sufficient oxygen for the life that might become imprisoned under the ice, and winter stagnation does not occur. If the lake does not freeze, the water may circulate throughout the winter. If it does freeze, the ice melts with the approach of spring, and circulation resumes. In either case, overturn in the spring will induce the plankton to increase.

Development from Oligotrophic to Eutrophic

As time passes, oligotrophic lakes will fill in by the two processes previously mentioned. Their sides may also be eroded away to some extent and thereby help to fill in the deeper parts of the basin. Exactly when a lake passes from the oligotrophic to the eutrophic stage is difficult to determine, for there is great variation of physical and biological conditions in lakes. One criterion that has been used to designate eutrophic lakes is that they possess a hypolimnion smaller than the epilimnion (Fig. 7-8). It is not always easy to use this criterion, however, since thermoclines may not develop every summer, especially in shallower lakes. When a thermocline forms, the hypolimnion may be so small and organic materials so abundant that stagnation occurs in the hypolimnion.

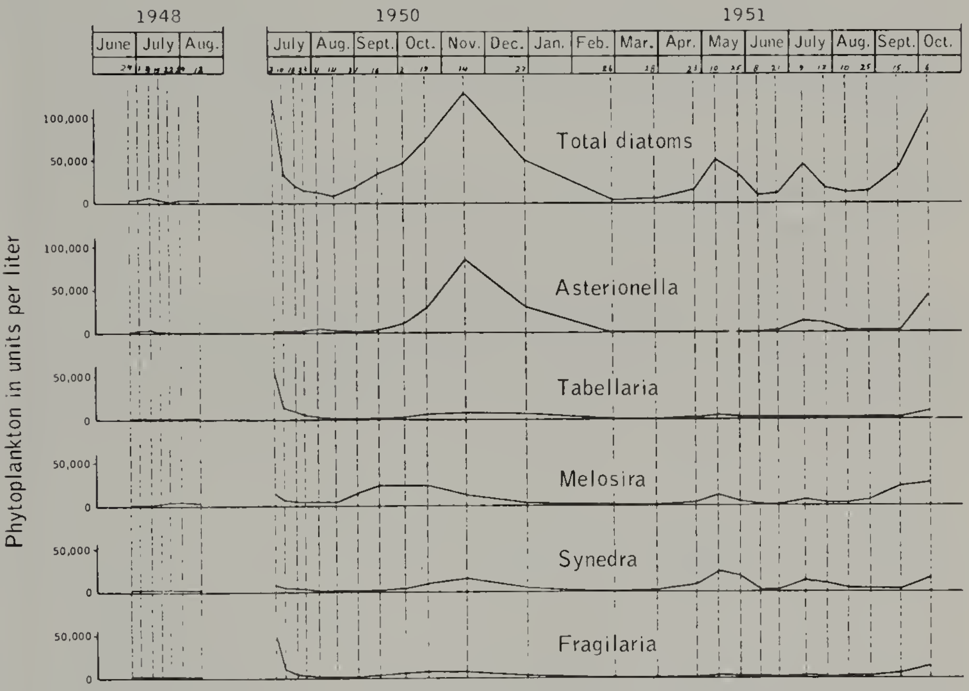


Fig. 7-11 Seasonal variation in standing crops of total diatoms and the major genera of this class in Douglas Lake, Michigan, during the summer of 1948 and from July 3, 1950 to October 6, 1951. Fall overturn began between September 16 and October 2, 1950. Ice appeared November 24, 1950; ice disappeared April 13, 1951. Thermal stratification began between May 10 and May 25, 1951. Fall overturn began between September 15 and October 6, 1951. From Tucker, A. 1957. The relation of phytoplankton periodicity to the nature of the physicochemical environment with special reference to phosphorus. II. Seasonal and vertical distribution of the phytoplankton in relation to the environment. *Am. Midland Naturalist,* 57:334–370.

Life and Seasonal Changes in Eutrophic Lakes

Life is abundant in eutrophic lakes, and plankton populations become especially high in the spring and fall (Fig. 7-12). In Clear Lake, California, Goldman and Wetzel (1963) found a large standing crop of phytoplankton, despite high turbidity and a consequent shallow penetration of light sufficient for photosynthesis (seldom below 12 feet). In this lake the spring phytoplankton productivity was not as great as the autumnal. Lakes may vary with respect to the dominant phytoplankton species present. Thus Tucker (1957) found in Michigan lakes that some were dominated by diatoms, some by golden algae, others by blue-green algae. Among the zooplankton of eutrophic lakes, rotifers may be the dominant type, as well as cladocerans, copepods, and protozoa. Since zooplankton feed on phytoplankton, their populations may be determined by phytoplankton populations, but probably in a complex way. For example, the rate at which certain species of copepods lay eggs in some lakes is related to the abundance of phytoplankton, but other past conditions probably affect egg-laying even more (Edmondson et al., 1962).

Organisms in the profundal zone may be numerous, but not very varied in species, especially in the oxygen-low hypolimnion. Thus in Lake Providence, Louisiana, where the profundal benthos is limited mainly to Chironomidae (midges), *Chaoborus* (phantom midges), and Oligochaetes (worms),

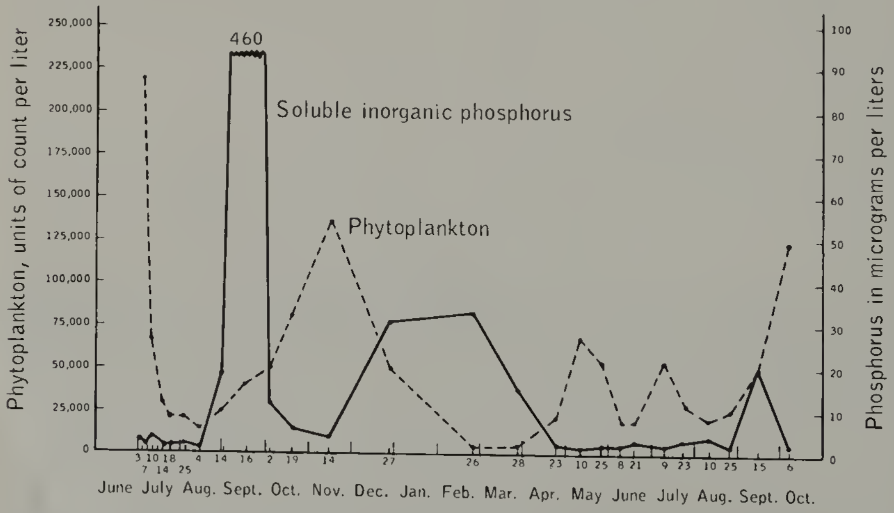


Fig. 7-12 Seasonal variation of standing crop of total phytoplankton and soluble inorganic phosphorus at 20-meter depth in Douglas Lake, Michigan. Years 1950–1951. See explanation of Fig. 7-11. From Tucker, *op. cit.*

Moore (1950) noted a high summer productivity as indicated by a standing crop averaging 90.4 pounds per acre. Typical fish of the profundal zone include pike, large-mouth bass, and catfish, and in the shallower areas bluegill, sunfish, and perch.

Of special concern to plankton of eutrophic lakes is the ability to maintain a certain position in the lake. Phytoplankton, for example, are able to produce food only in the upper levels where there is adequate light. If they descend too far, they will eventually die. Similarly, if zooplankton fall below their food supply (the phytoplankton), they will be in difficulty. Recalling what has been said concerning temperature and density gradients and the effects of thermal stratification on circulation of water in lakes will indicate the complexity of the problem. The situation is especially serious for plankton of eutrophic lakes because of the stagnation of the hypolimnion. The density of the protoplasm of plankton is such that the organisms tend to sink. However, certain devices either act as floats or increase friction to slow down sinking movements. Thus hairs, spines, attachment of individuals into colonies, air floats, and oil bubbles are among the various devices which help them stay in the limnetic community.

Some of the benthos in the profundal zone have solved the flotation problem remarkably well. These animals exist as members of the benthos only during the day, rising to the surface in the limnetic zone by night. Thus Woodmansee and Grantham (1961) found that in Lake Geiger, Mississippi, the majority of the population of *Mesocyclops edax,* a copepod, and *Chaoborus albatus* spent daylight hours in the oxygen-deficient hypolimnion, and at night both populations moved into oxygenated water.

In eutrophic lakes, the thermocline may become established in early May and remain until mid-September, as in Lake Douglas, Michigan (Tucker, 1957), and Lake Providence, Louisiana (Moore, 1950). The upper limit of the thermocline may descend 9 to 15 feet during the summer, depending on the geographical location and physical conditions of the lake. As this occurs, the hypolimnion becomes smaller, since the thermocline does not usually vary in thickness this much. Oxygen may be thoroughly depleted by July as bacteria use it in decomposing dead organisms, and animals use it in respiration. After the oxygen has been used up, phosphorus, nitrogen, and other nutrient elements are slowly released from iron compounds on which they were formerly adsorbed or united with chemically. Since it may take up to eight weeks for this release to be completed, the sooner oxygen is depleted, and the longer the thermocline lasts, the more complete will be the release of the minerals into solution in the hypolimnion (Tucker, 1957). The greater the amount of minerals that are released, the larger may be the plankton bloom when overturn once again brings these substances into the limnetic zone. However, in Douglas Lake, when the overturn occurs, phosphorus does not increase in the upper water. Although there are several possible explanations for this anomaly, none are fully satisfactory (Tucker, 1957).

The fall overturn will bring an upsurge in the plankton bloom, which will decline with the approach of winter. If eutrophic lakes freeze over, the situation of aquatic organisms becomes grim. With a smaller total volume of water than the oligotrophic lake and a much higher total population of organisms, oxygen may become extremely scarce. If the ice cover remains for a long time, especially if a cover of snow prevents light penetration and photosynthesis is thus reduced, great destruction of life may occur. Decomposition of the abundant organic matter in the water and on the bottom adds to the difficulties by further depleting the oxygen supply, although some oxygen is being continually added by phytoplankton and rooted plants of the shore zone. When spring arrives, the overturn again allows the entire lake to benefit from the nutrients on the bottom and the oxygen from the atmosphere.

Development of Eutrophic Lake to Dry Land

As eutrophic lakes continue to become shallower, they reach a point at which thermoclines never form, and circulation occurs throughout the summer. The entire volume of water may become quite warm at this time. Rooted aquatics usually become established, even in the deepest parts of the lake (Fig. 7-14). This stage of vegetation-choked water, sometimes called the *senescent* stage, is highly productive. Small fishes, frogs, water snakes, and turtles may abound, as well as a host of insects and other invertebrates (Fig. 7-13).

When the senescent lake becomes shallower, it may become a pond; that is, merely a smaller area of open water. Or it may develop directly into a swamp or marsh. A swamp is usually considered to contain trees, while a marsh, by definition, does not. Ponds may become so shallow that they dry

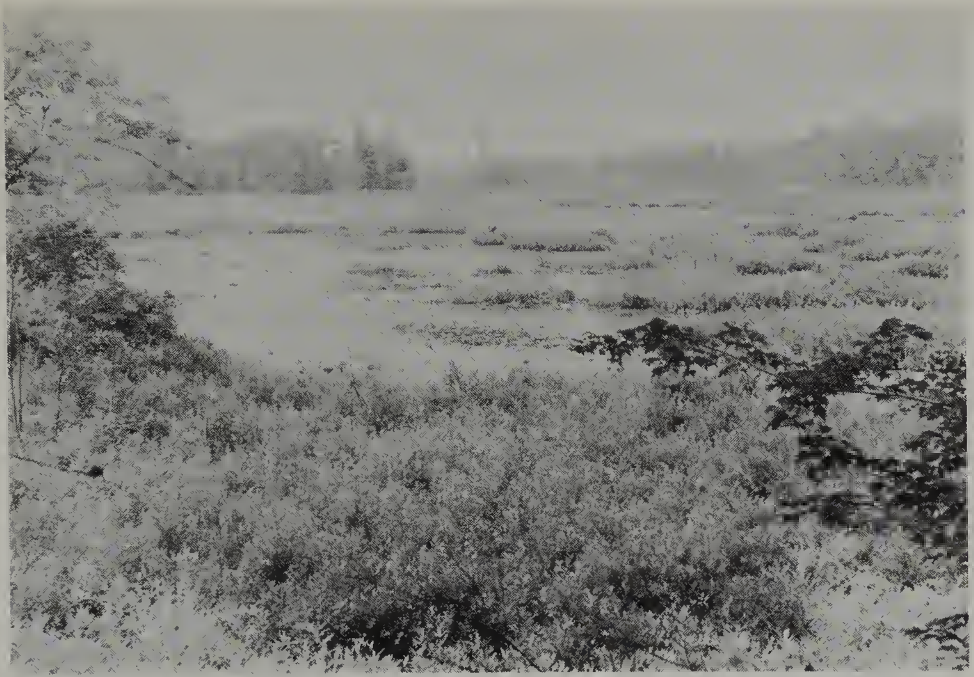


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Fig. 7-13 A lake in the senescent stage with emergent vegetation growing throughout. Near Petersham, Massachusetts.

up in the summer months, thus becoming temporary ponds (Fig. 7-15), unsuitable for occupation by permanently aquatic animals. Because of this major change in environment, forms of life are more limited, although many insects and other animals may be common. Plants growing here are predominantly emergents (plants which live with their roots submerged in water but whose vegetative and flowering parts are mostly above the water). Cattails, arrowheads, pickerel weeds, and various kinds of sedges and rushes are among the most abundant of them. Certain invertebrates are of interest because they are found in temporary ponds. Among the widely distributed members of this group are the fairy shrimps of the genus *Eubranchipus.* Some relatives of this genus are able to live in temporary alkaline or saline pools in the West. Because of the temporary nature of these ponds, many of the larger predatory species are absent.

Eventually the pond, marsh, or swamp will dry up completely as terrestrial plants and animals invade the site of the former lake. Bushes, trees, and herbaceous plants which are tolerant of soggy ground will add their remains to the soil, until conditions become sufficiently mesic to tolerate a purely

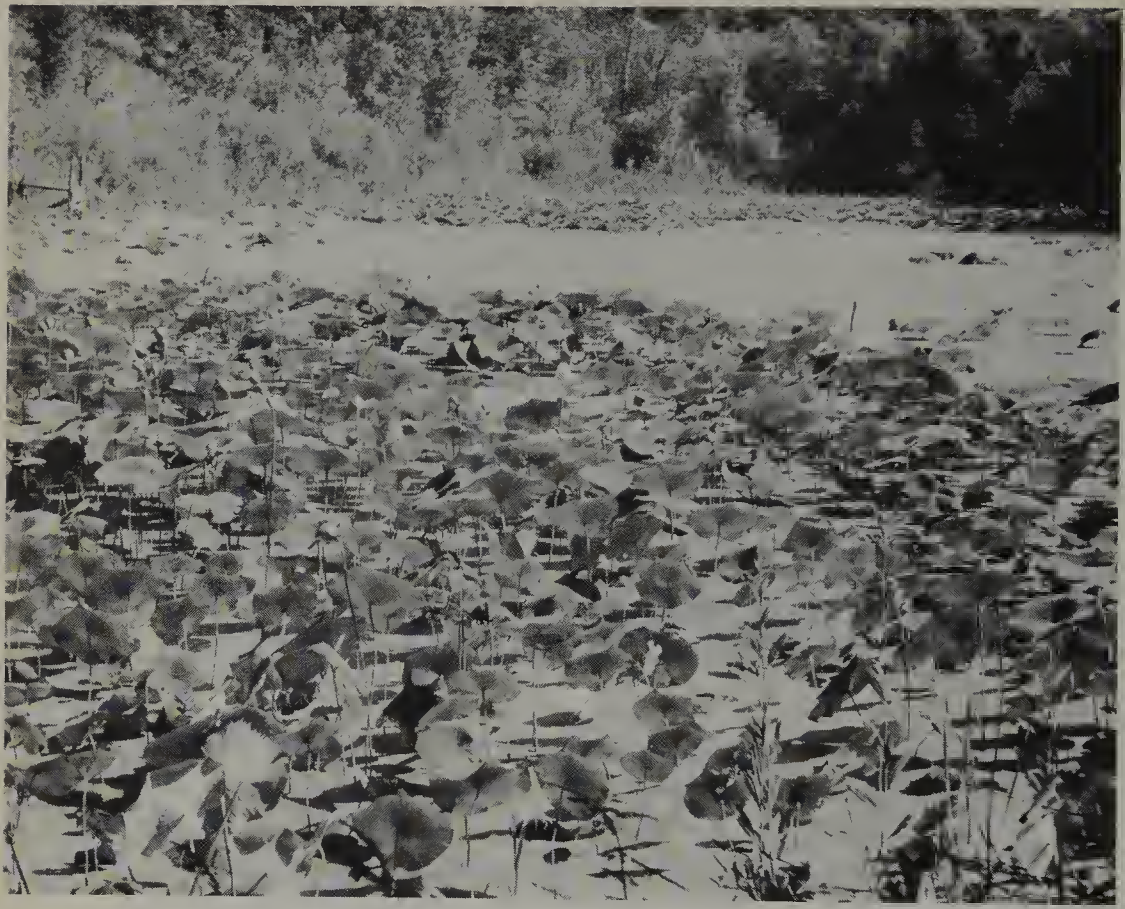

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Fig. 7-14 Vegetation-choked stage of a eutrophic lake. The large plant is the lotus, *Nelumbo lutea*. The water around these plants is covered by duckweed, *Lemna minor*. Macoupin County, Ill.

terrestrial community. Finally, the end of the eutrophic-lake succession is the terrestrial climax community (Fig. 7-16).

Conditions in Dystrophic Lakes

Dystrophic lakes proceed along a different line of succession. They are frequently formed as the result of glacial action similar to that which forms some oligotrophic lakes. Owing to physical and chemical states which prevent the decay of organic materials, biotic conditions in such lakes are different, and succession takes a different course. Calcium and oxygen are usually deficient, and the pH of the water is generally low. The abundant organic matter of the water is in the form of undecayed organisms which create deposits of peat

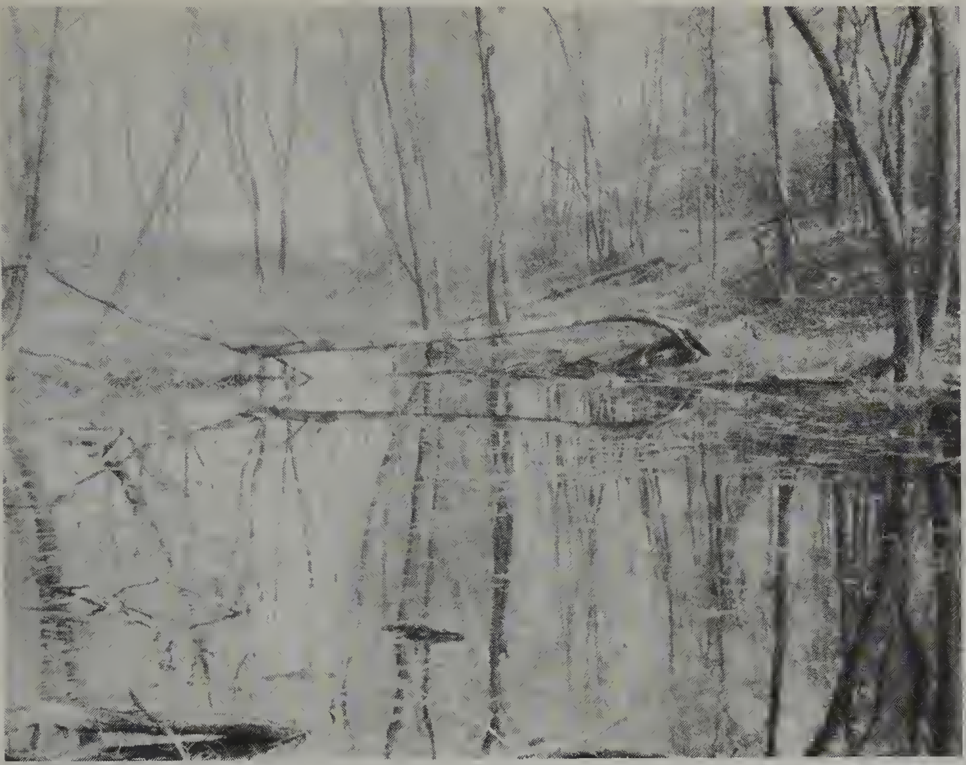

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Fig. 7-15 A temporary pond which will dry up completely during the summer. In spring it serves as a home for the fairy shrimp, *Eubranchipus*, and as a breeding place for amphibians. Macoupin County, Ill.

on the bottom and frequently impart to the water a brown stain.

Dystrophic lakes are usually poor in numbers and types of organisms. Larger plants, e.g., *Chara*, which remove calcium from the water, may be present, but in general the phytoplankton and rooted aquatics are scarce. Zooplankton may be numerous, but larger invertebrates are frequently low in abundance, as are such vertebrates as the fishes. Sphagnum moss is the typical plant found growing in the beach or shore (psammolittoral) zone of these lakes, along with sedges and other plants which form a mat.

Development of Dystrophic Lakes to Dry Land

As the dystrophic lake accumulates peat on the bottom, it hastens its own end. The sphagnum and rooted vegetation of the shores may grow out into the water, advancing over the surface of the lake. It is thereby developing into a peat bog,

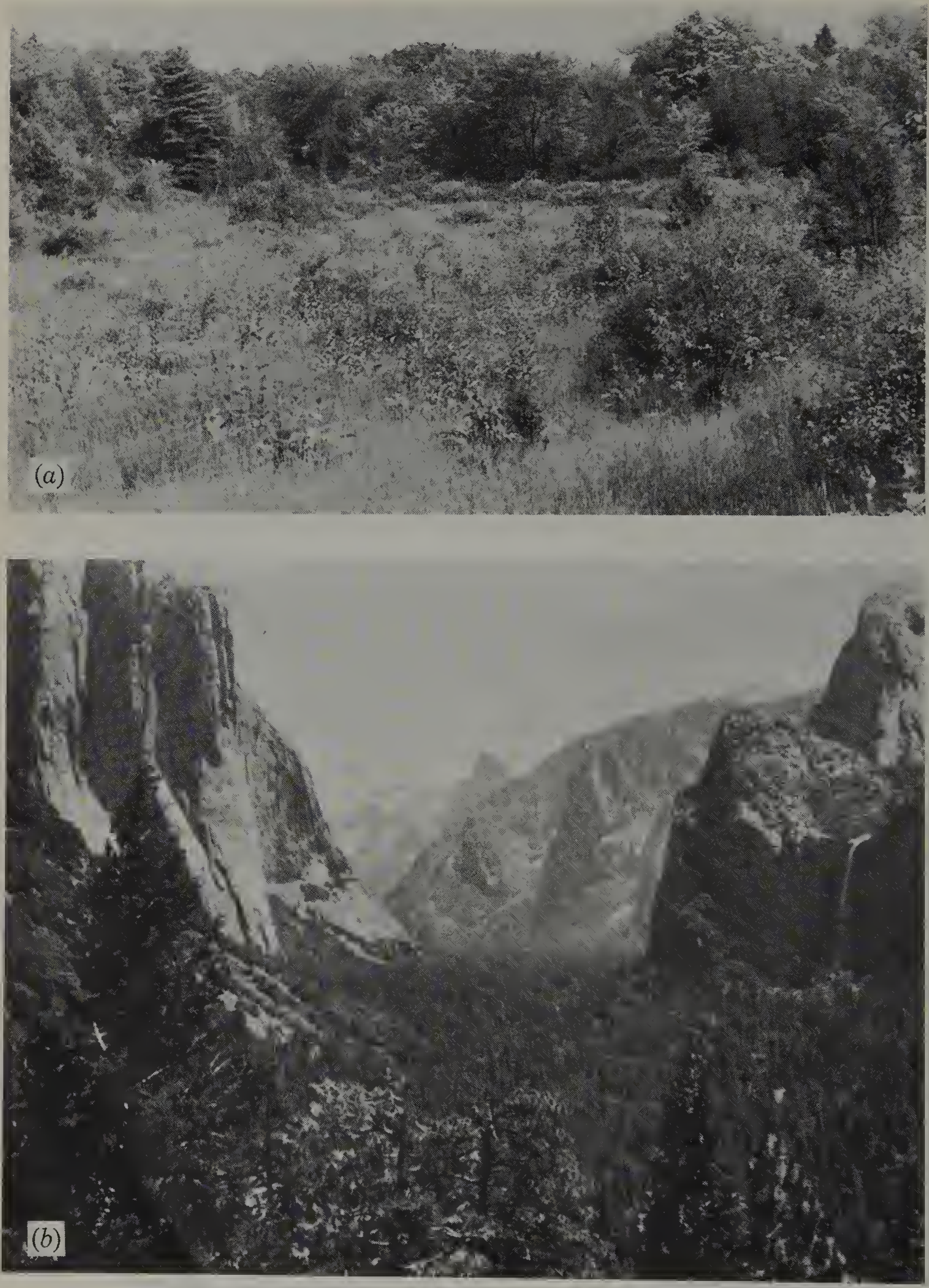

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Fig. 7-16 Terrestrial succession on the site of former lakes: (*a*) Early stages of succession in a moist area which has not been long dry. (*b*) A coniferous forest on the site of a former glacial lake, Yosemite Valley, California.

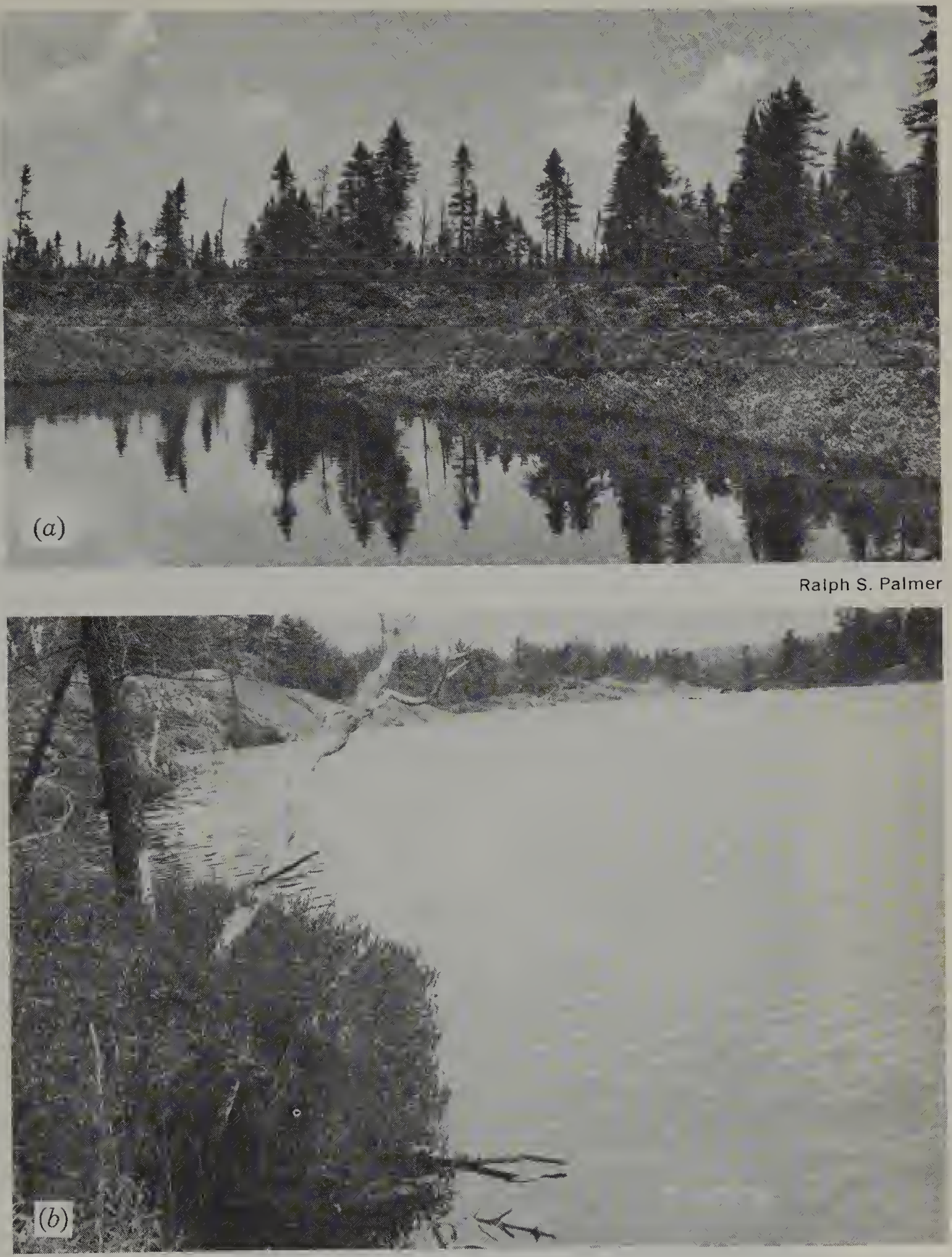

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Fig. 7-17 Development of dystrophic lakes:

(*a*) A dystrophic lake in Maine in the pond stage, with quaking mat well out over the water.
(*b*) A dystrophic lake in Ontario, Canada, in early stage of succession. A vegetation mat is just beginning to grow out over water at left.

with a shore of vegetation forming a quaking mat, and a bog lake in the center (Fig. 7-17*a*, *b*).

The surface mat eventually closes over the bog lake, and sphagnum and other vegetation fill up the basin. The outstanding physical condition of such a community is the low pH of the saturated "soil" of the mat, which is sometimes less than 4.0. A variety of plants are especially adapted to these conditions of moisture and low pH, and these make up the bog community. Here we find the insectivorous pitcher plants (*Sarracenia*) (Fig. 7-18) and sundews (*Drosera*); cranberry (*Vaccinium oxycoccus*) and cotton grass (*Eriophorum*) (Fig. 7-19). Shrubs which invade the bog usually include leatherleaf (*Chamaedaphne*), Labrador tea (*Ledum*), and bog rose-

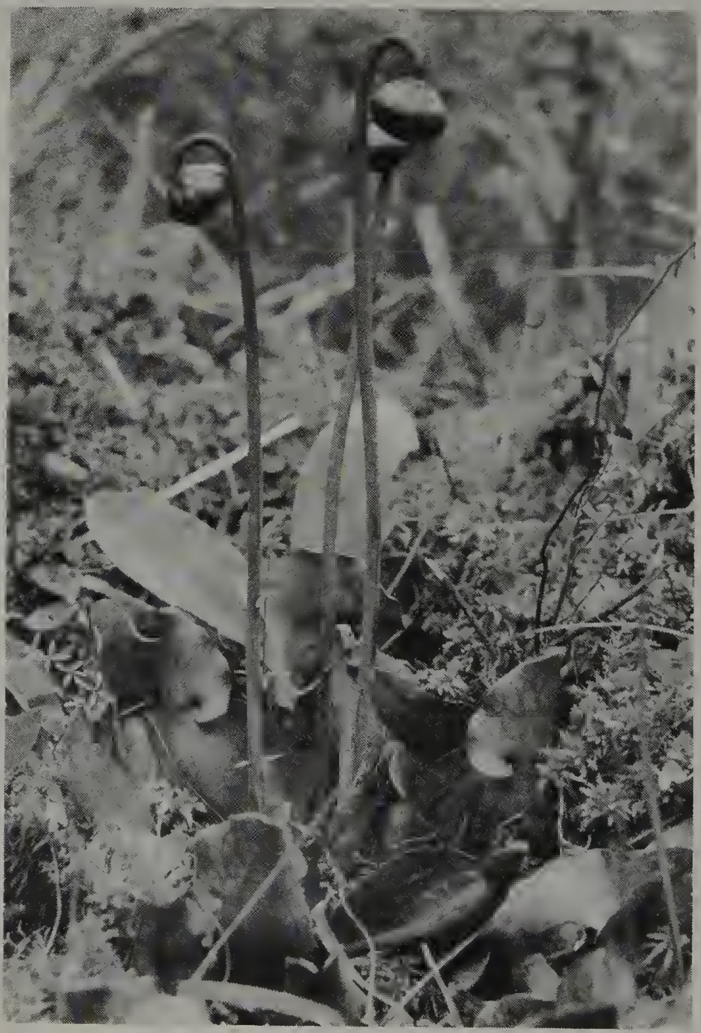

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Fig. 7-18 Typical bog plant, the pitcher plant, *Sarracenia purpurea.*

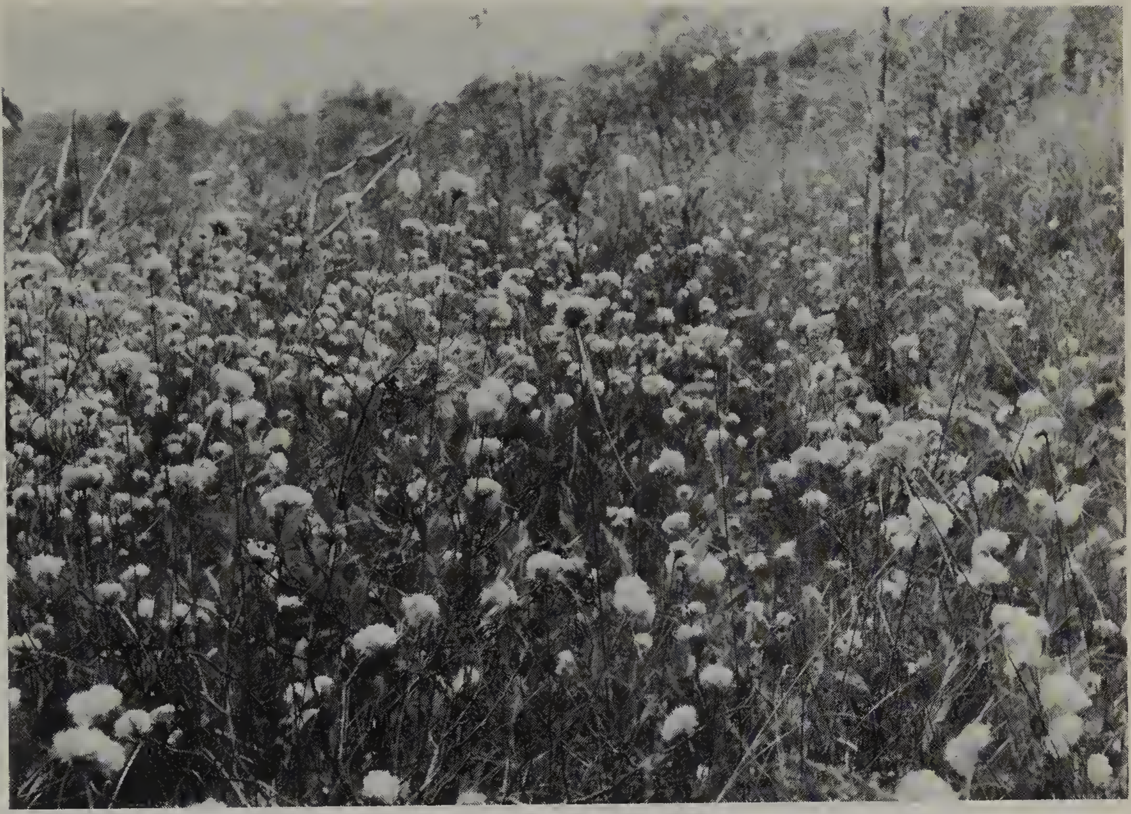

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Fig. 7-19 Cotton grass, *Eriophorum*, a typical genus in northern and arctic bogs, here growing in a marsh in western Maryland at an altitude of about 3,000 feet.

mary (*Andromeda*). Several species of orchids are restricted to this habitat. Diatoms and certain species of algae may be found among the saturated sphagnum.

Eventually the basin will be further filled by encroaching bushes and by the dead bodies of plants and animals, until finally the terrestrial climax community covers it. The length of time required for this to occur varies widely, depending on such variables as the original depth of the basin, its drainage, and other physical conditions which affect the growth of organisms and the rate of sedimentation. As in the succession of oligotrophic lakes, a series of communities has been established and changed, each one replacing the preceding one, until eventually the climax is reached.

ZONATION OF AQUATIC COMMUNITIES

Along the edges of eutrophic, oligotrophic, and senescent lakes, there may be shores which descend gradually to the depths of the lake, with bottoms of sand, mud, gravel, or clay. Frequently aquatic vegetation will be found growing here, and a whole series of communities may be formed. Floating aquatics will occupy the deep water, and various kinds of rooted vegetation will follow in regular sequence up to the beach. These communities show a zonation similar to that of vegetation on a mountain, except that it occurs for a much shorter distance and is therefore more easily observed. In effect, this zonation illustrates the process of succession in lakes. It is possible to observe from it how lakes become more shallow by the action of such communities and how the changing depth of the water affects the composition of the communities.

Small Floating Aquatics

The areas of lakes involved in zonation include the littoral zone (the region in which there is light penetration to the bottom) and the psammolittoral zone (the region along the edge of the water). The deepest water of the littoral zone may have a surface cover of small floating plants such as the duckweeds—*Lemna*, *Wolffia*, and *Spirodela*. Sometimes these plants will cover a small lake or pond (Fig. 7-20). Of course, in this region as in most of the succeeding ones there are plankton and nekton populations. Where the water is shallower, perhaps 20 feet or less, some rooted aquatics may be found, including *Vallisneria*, *Anacharis*, *Myriophyllum*, and *Ceratophyllum*. These are all totally submerged plants. One of the largest and most abundant groups of submerged aquatic plants found in the littoral zone belongs to the genus *Potamogeton*, which includes more than 50 species in North America.

Rooted Floating Aquatics

As the depth of the water decreases toward the shore, a zone containing a community dominated by rooted floating aquatics will be found (Fig. 7-21) Typical of such plants are white water lilies (*Nymphaea*), the cow lily (*Nuphar*), and *Potamogeton natans*. Many animals are associated with these

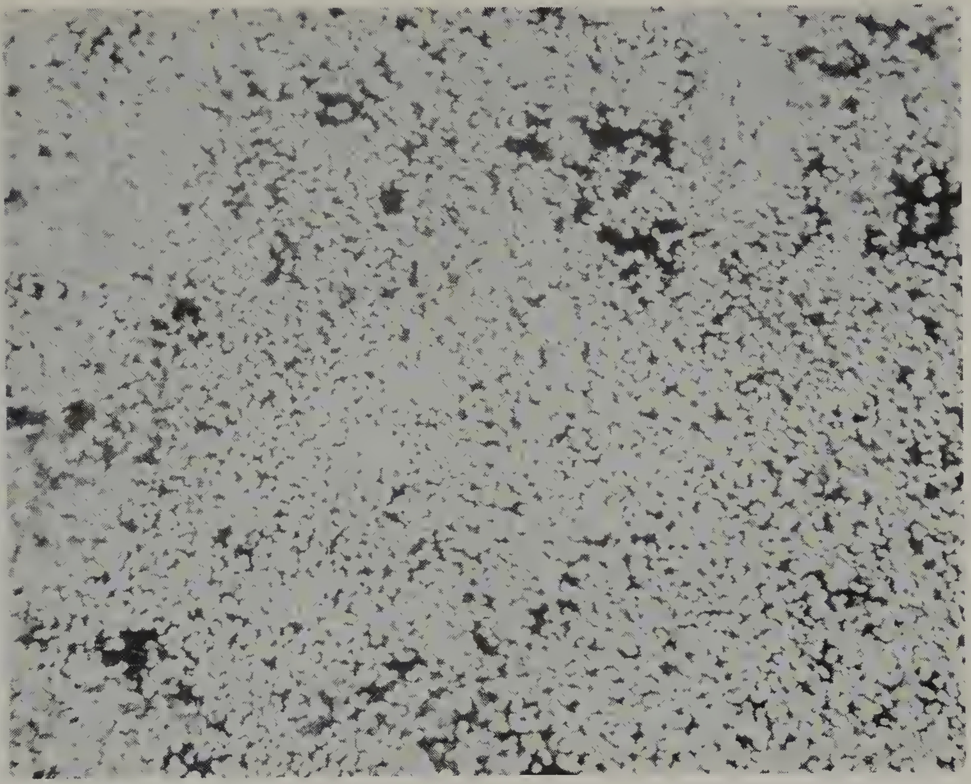

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Fig. 7-20 Duckweed, *Lemna minor,* covering the surface of a pond.

plants, using them as places for support as well as for food. Many herbivores feeding on the phytoplankton are present, while carnivores are there to feed on the herbivores. For example, the small fresh-water coelenterate *Hydra* may often be found hanging downward from the undersurfaces of pond lily pads. This little animal extends its tentacles into the water to catch small water animals such as insects, copepods, and cladocerans. These in turn feed on protozoa, bacteria, and minute algae (Pennak, 1953).

Emergents

In shallower water, a zone may occur possessing a community dominated by emergent plants. These species have their roots and lower stems in water, but most of the plant projects into the air. Some of the more common species of this community are cattails (*Typha*) (Fig. 7-22), bulrushes (*Scirpus*), reed grass (*Phragmites*), and wild rice (*Zizania*). In this zone the bottom is usually abundantly covered with the

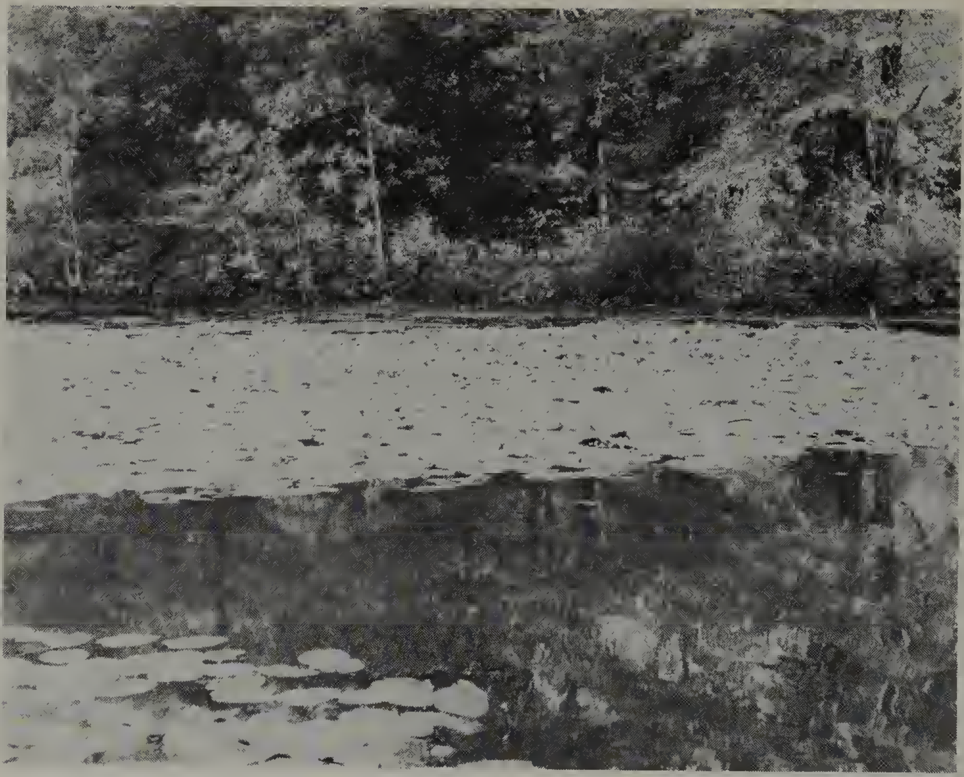

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Fig. 7-21 Zone of rooted floating aquatics, white water lilies, *Nymphea odorata*, and cow lily, *Nuphar advena*. Lake Huron, Canada.

rotting organic debris of the old emergent plants, and this forms a situation favorable to small animals. Insect larvae such as dragonflies, damsel flies, and adult and larval beetles and bugs may abound in the mud and water, along with a rich zooplankton. Larger forms such as frogs, salamanders, turtles, and water snakes may inhabit this community. Certain fishes like the bullhead (*Amieurus*) and the mud minnow (*Umbra*) are often present.

Saturated-soil Regions

Next to the shoreline, there is frequently a region in which the soil is saturated with water. Here a community exists in which the dominant plants are various sedges (*Carex*), rushes (*Juncus*), smartweeds (*Polygonum*), and many others (Fig. 7-23). This community may have a large number of microscopic plants and animals, so that the water edge, or psammolittoral zone, may possess the most densely populated community of all the zones.

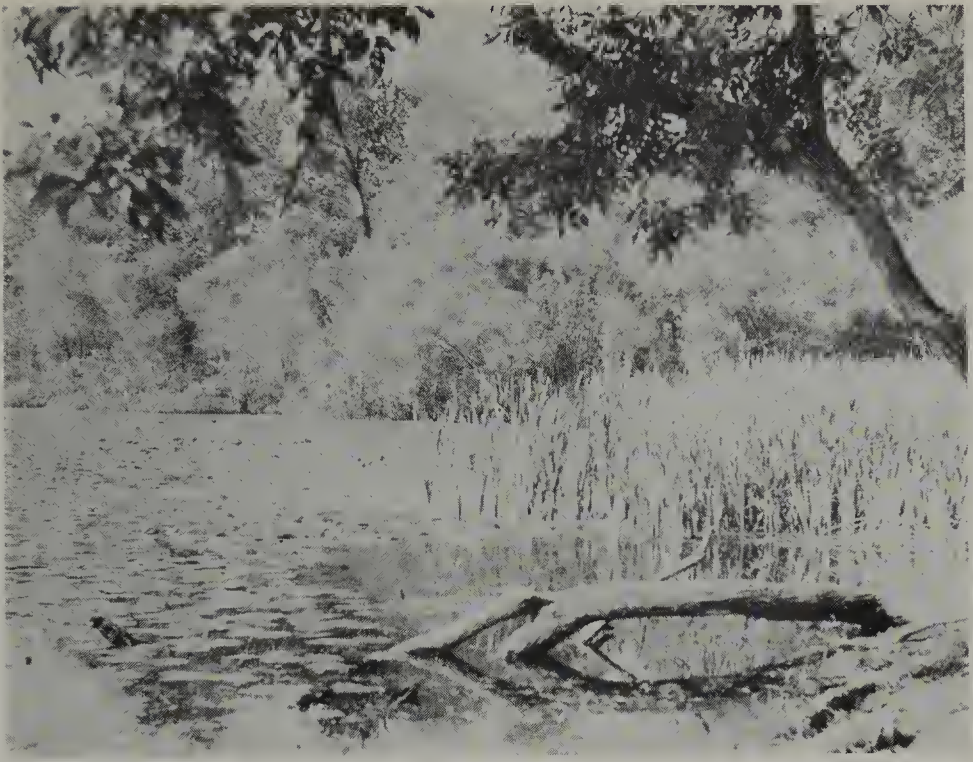

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Fig. 7-22 Floating rooted aquatics, *Nymphaea odorata;* emergents, here mostly cattails, *Typha*, advancing toward the center of the pond. Albany, N.Y.

Shore Communities

On drier land, farther from the shoreline, is a community dominated by rank herbs. Water is still abundant in the soil. Wild hemp (*Cannabis*), sunflowers (*Helianthus*), jewelweed (*Impatiens*), joe-pye weed (*Eupatorium purpureum*), and boneset (*Eupatorium perfoliatum*) may be among the common plants (Fig. 7-24). Animals are those of the terrestrial communities which can forage into the wetter locations. Common species include field mice, shrews, raccoons, and weasels among the mammals, various nesting birds (Fig. 7-25), and frogs and snakes among the lower vertebrates. Hordes of insects also constitute an important part of the community. Still farther back on land will be found the shrub community, with elderberry, red maple, box elder, cottonwood, willows, alder, and viburnum among the forms represented. A few shrubs such as the buttonbush may grow in more aquatic situations, but these are scanty. From the shrub stage, the development to the climax community will be a sere similar to

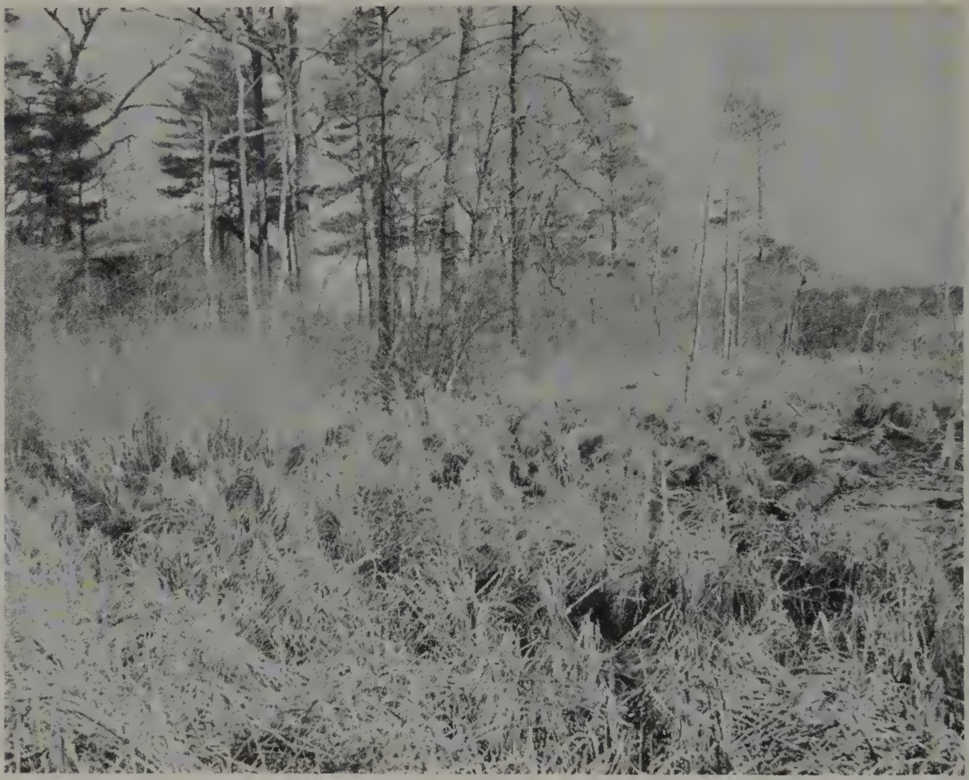

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Fig. 7-23 The region of saturated soil around the shore line of a pond, with sedges as the dominant plants.

the one described for terrestrial succession, with perhaps different dominants appearing in the various communities.

Evidences of Succession

The communities from the open water of the lake or pond through the littoral region to the climax on the shore may all be seen at one time; but they represent dynamic changes, which will eventually result in the filling in of the lake and the elimination of the communities. As time passes, each community will invade its neighbor toward the center of the lake. In all the communities, organic matter and silt are constantly accumulating, decreasing the depth of the water. With this change of environment each community invades the one next to it in deeper water and is in turn invaded by the one behind it in shallower water. Thus, as the filling process occurs, the submerged aquatic plants will be displaced by the floating rooted aquatics, and these by the emergent aquatics. As succession continues, the emergents will be replaced by

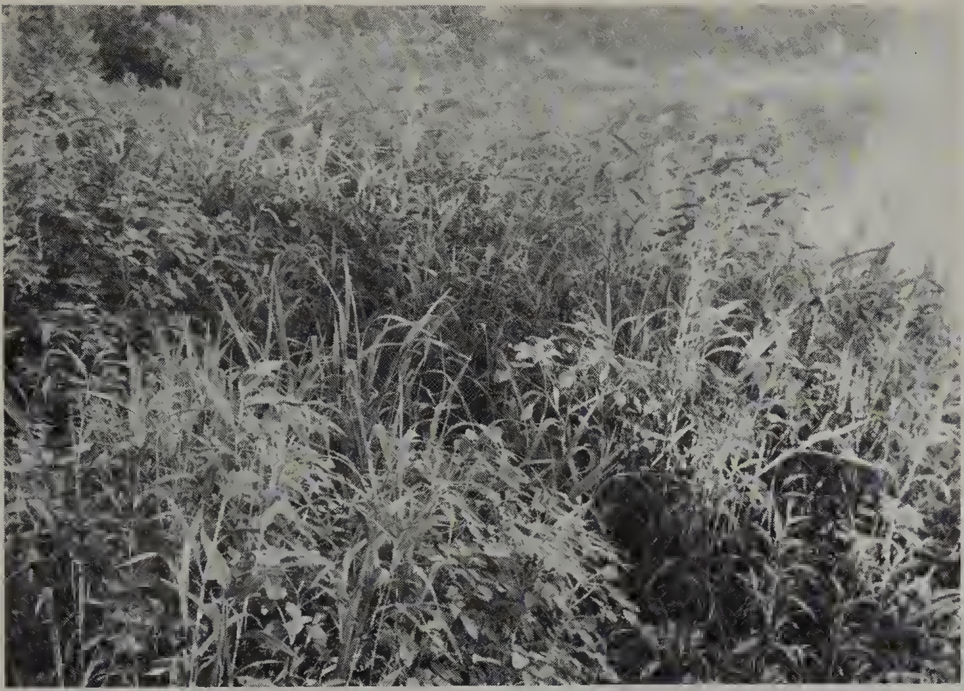

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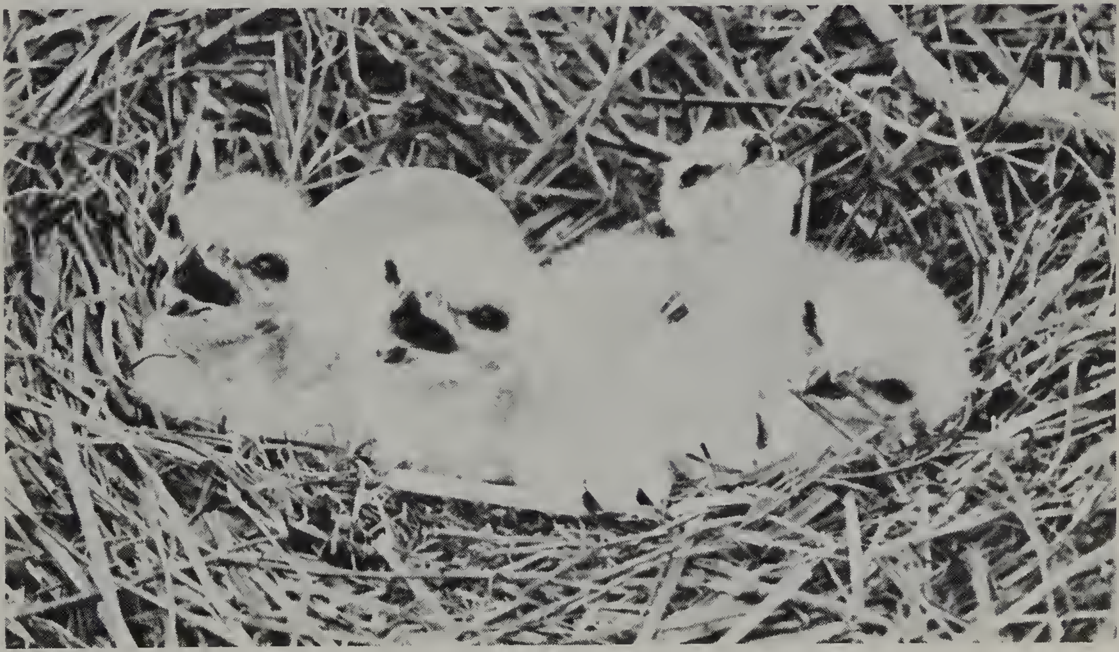
Fig. 7-24 Rank vegetation in the damp soil near the edge of a pond. Jewelweed and smartweed are dominants.



E. G. Tabor

Fig. 7-25 Marshes are nesting sites for many birds. Grassy marshes are preferred breeding habitat for the marsh hawk, *Circus cyaneus*, whose young are shown here in the nest.

sedges and rushes, and these in turn by rank herbs and shrubs. Gradually the terrestrial communities will move in where once there was open water, until finally the terrestrial community climax occupies the area.

The communities of plants and animals in the sere are similar in various kinds of lentic environments, although the species may vary. For example, muddy bottoms may support different plants and animals than gravel bottoms, and on shore the species found on sandy beaches may be different from those on rocky beaches (Fig. 7-26). Thus the species composition of similar communities will vary with different environmental conditions, but the general pattern of the succession will be about the same.

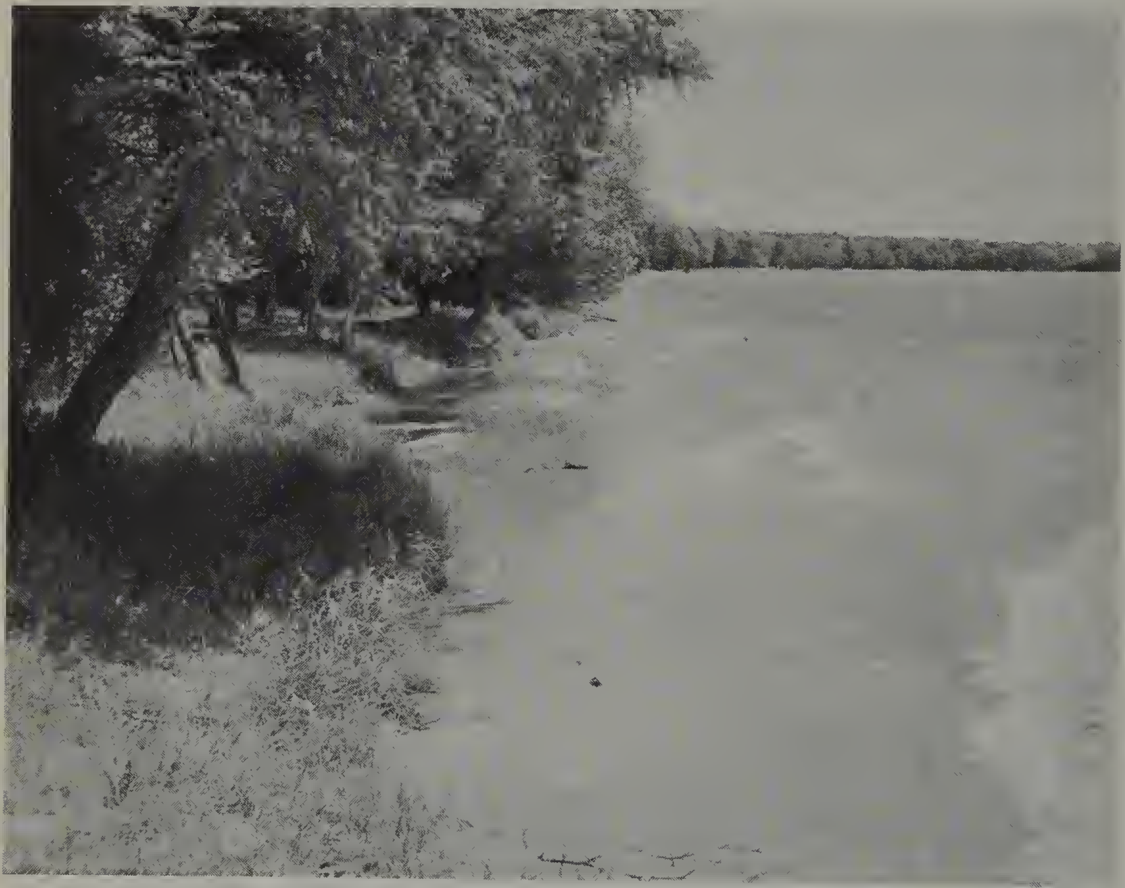


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Fig. 7-26 Sandy beach on a wave-swept shore. Notice that there is no large aquatic vegetation. Higgins Lake, Mich.

STREAM SUCCESSION

The development of streams is quite different from that of lakes and other lentic environments. Whereas in the succession we have reviewed above, organisms help to bring about the successional changes to a great degree, in lotic environmental evolution, physical forces play the dominant and almost exclusive role. Since physical forces, therefore, shape the development of biological communities in streams, the physical evolution of streams will be considered first.

Stream Gradient

In a flat world there would be no streams, for the water in streams is flowing from an area of higher elevation to an area of lower elevation, and ultimately to the sea. The difference in elevation from the origin of a stream to its terminus, divided by the distance it travels between these two points, gives the average elevation gradient of the stream. The greater the gradient, the greater should be the rate of flow, all other factors being equal.

When a land mass is newly elevated, the water will run off the surface into the natural depressions which are present and eventually find its way to the ocean. At first, many of these depressions may hold water as ponds or lakes, but with their filling and the erosion of their outlets, they tend to be obliterated. At the same time, the streams may be small and, if the elevation gradient is large, proportionately swift. Such a swift stream is able to carry or move large rocks as well as gravel and silt from the hills to the plains. This load, combined with the washing action of the water, will wear down the stream bed as its smaller tributaries are wearing down their stream beds and the surrounding hills. In effect, the hills are being slowly carried to the sea. As this occurs, the stream at any given point becomes larger, the stream bed lower, and the stream as a whole longer. Another result is that the elevation gradient is decreased and the flow slackened at any given point along the stream, a process called *base leveling*.

As long as the rate of flow remains fairly high, the stream will carry a load of soil eroded from the more elevated regions. As the rate of flow decreases, the size of the particles it carries will decrease, until finally only silt will be held in suspension when the flow becomes sluggish. When the stream, which by now has perhaps developed into a river, empties into the ocean, the final precipitation of the finely divided particles of earth will occur, forming deltas which may be of vast extent.

If it were possible to watch long enough, a single location along a stream could be observed and the process of change from a swift stream to a sluggish one could be recorded. But this would require many centuries or even thousands of years. Fortunately for the ecologist, however, this succession may be observed in a short period of time just as we can observe the various communities involved in the succession of lakes. In the latter case, we look at different lakes in varying stages of development, or we study the zonation of littoral communities. With streams one merely needs to travel the length of any one to see the various seral stages in its succession. Thus the headwaters of the stream possess the aspects of a young stream, the larger and slower regions an intermediate stage; and finally, where the stream becomes a deep river, the characteristics of a mature stream are present. Therefore, as a stream accomplishes base leveling, organisms once able to live only in the lower parts of the stream are able to move upstream into the tributaries (Adams, 1901). The physiographic changes occurring with base leveling of streams thus allow a special type of succession to occur (Shelford, 1911).

Physical Conditions in Swift Streams

In the headwaters, various physical factors which are interrelated with the swiftness of the current are important to the life of the stream. There is a tendency toward large fluctuations in volume and flow of water from season to season. During the spring especially, small streams are unusually swollen. During the summer, these same streams may become almost completely dry. Such extreme variations require special means for organisms to remain in place and to survive under widely different conditions. The swift current can carry away small particles of rock so that, in general, the swifter the stream, the larger the rocks remaining in its bed (Fig. 7-27*a*, *b*). The large rocks form places of shelter and attachment for organisms, although even these big boulders may be moved during high water.

The bottom is normally composed of rocks and pebbles of various sizes, and occasionally, as on the inside of a bend, of gravel or sand. The water of swift streams reflects this bottom type and is clear, except during flood stage. There are,

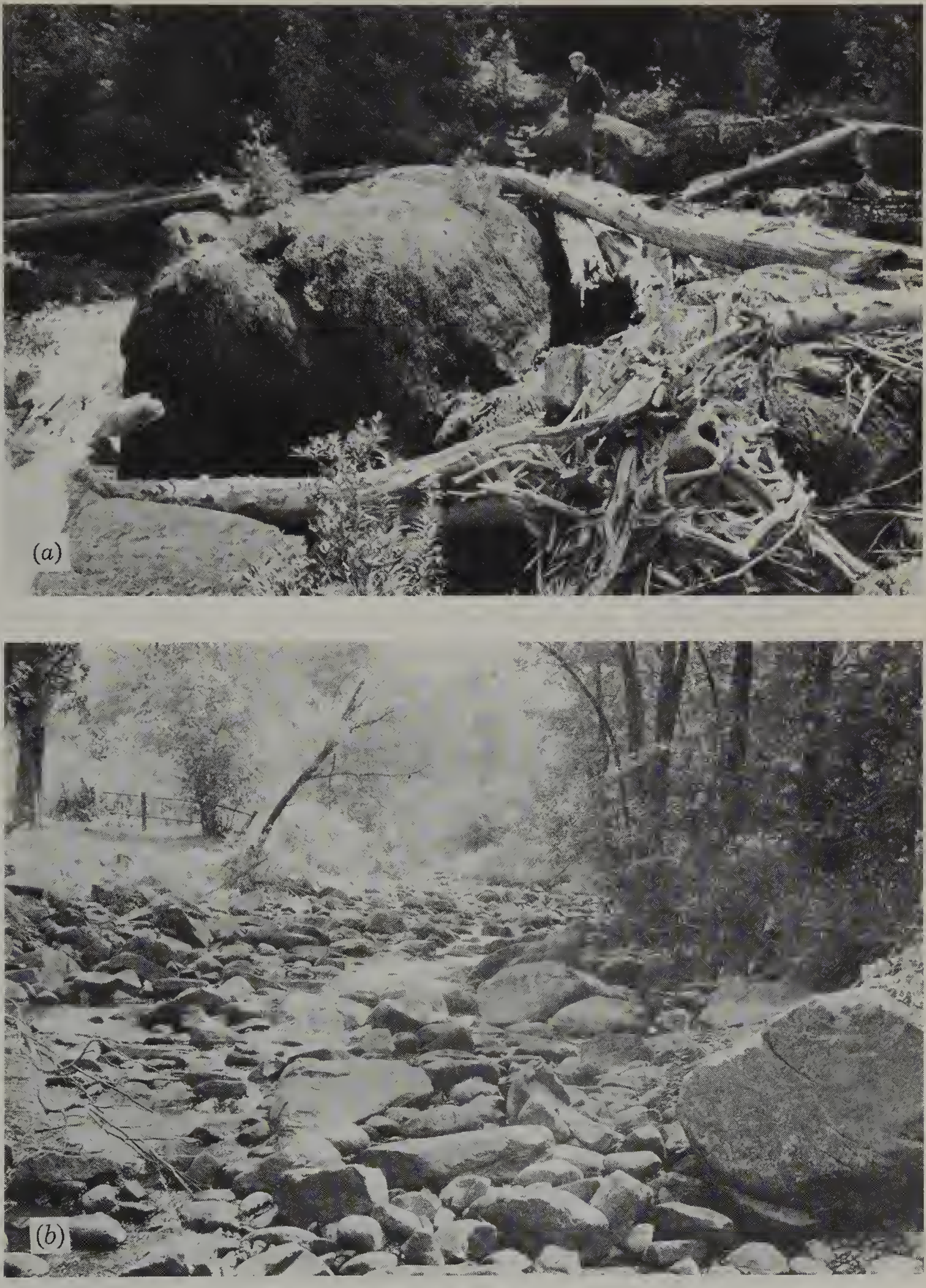

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Fig. 7-27 Effect of swiftness of current on size of rocks in stream bed:
(*a*) Huge boulders in a mountain stream.
(*b*) Large rocks and boulders in a swift stream.

in other words, relatively small amounts of finely divided soil particles or organic matter in the water. In occasional pools, however, several conditions are different from those found in the riffles. Among others, current may be reduced, and therefore deposition of fine particles may occur, which thus changes the bottom type in these locations to mud or silt.

Although the current flows swiftly in headwaters, it is usually relatively shallow, with only occasional deep pools. These conditions, too, affect the biota. The shallowness of the water permits excellent aeration (Fig. 7-28), but it also means that the temperatures here may vary more or less with the temperature of the atmosphere. The only exception to this will be when the stream is covered with ice, at which time the temperature of the water is stabilized near the freezing point. Since the amount of carbon dioxide and oxygen that may be dissolved in water is directly affected by the temperature, it follows that there is a continual variation in the amounts of these gases in the water, except during the period when the stream is covered with ice. However, oxygen content of swift streams, because of constant aeration and cool temperatures, is usually high. Some stability of the water temperature is afforded by trees and shrubs that usually line

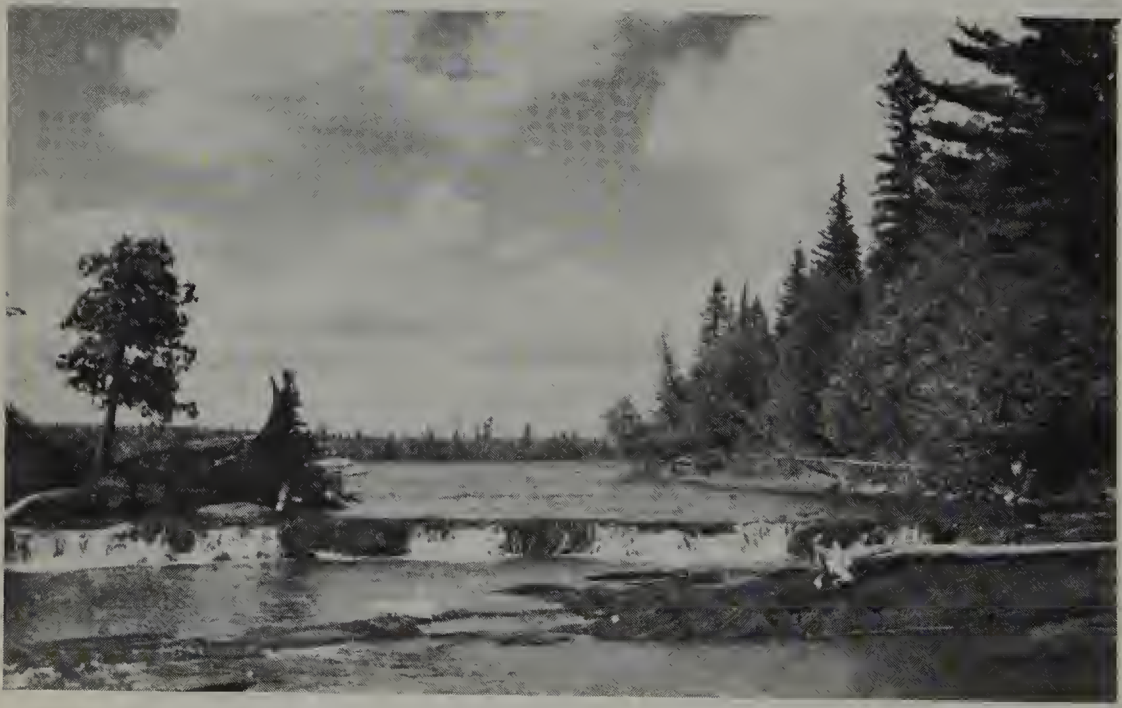

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Fig. 7-28 A shallow, swift stream permits excellent aeration of the water.

the banks of small, swift streams. Their shade prevents excessive warming by the sun, which would otherwise quickly heat the shallow water.

Adaptation for Swift-water Life

Because life in the swift streams is precarious or impossible for many organisms, the inhabitants of this environment are like the pioneers in other successions: they are able to endure severe environmental conditions. Various attributes of swift-water organisms enable them to survive the rigors of their habitat. They may have special hold-fast mechanisms, or a streamlined shape, special respiratory apparatus, or unique food-getting devices. In addition, many of the smaller forms must be able to reproduce rapidly, for the loss of life during the high-water period is great.

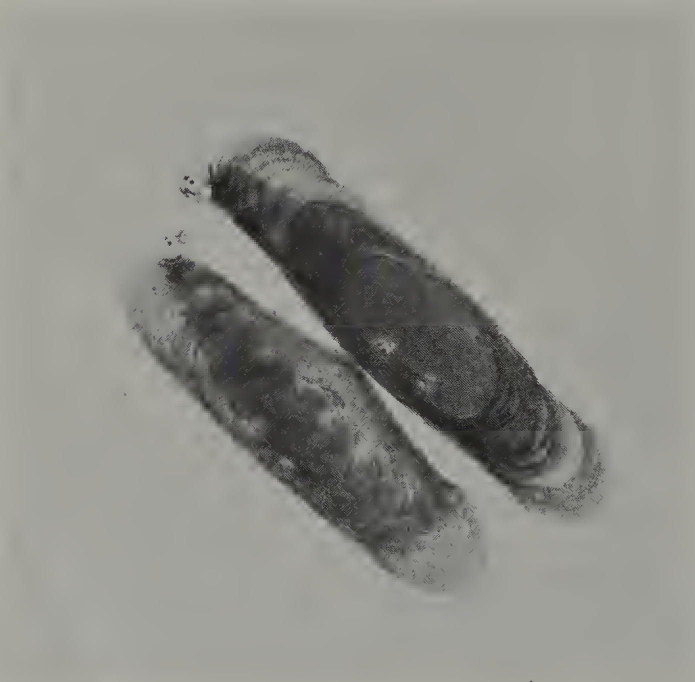
Permanently rooted aquatic plants are practically nonexistent in swift streams. Only in pools may a few such plants be found. The swiftness of the current makes attachment difficult, and the fluctuations in water level are also prohibitive to their existence. Instead, filamentous algae such as *Cladophora* and *Ulothrix* cling to the rocks by means of holdfasts; among their filaments are smaller algae such as diatoms and desmids. These minute plants are the basic food for all animals living in such water.

A group of plants found in streams which needs further study is fungi. Cooke (1961) found more than 90 species of soil fungi growing in a stream, and points out that fungi may have an important function in stream purification by aiding in reduction of organic waste materials.

The animals of this habitat are adapted either to swim against the current for short periods as they dart from rock to rock, or to cling by some means in open water or behind or under rocks. Their body forms frequently reflect the environmental conditions of their lives, in being streamlined or otherwise adapted for the least resistance to the friction of the water. One of the more abundant insects of this community is the black fly. Its larvae are frequently so numerous as to cover large areas of the rocks, giving them a velvety black appearance. These larvae are able to maintain their positions in fast water by means of an adhesive disk at their posterior ends. If they care to move, or if they are swept loose, they spin a silken lifeline from their mouths to prevent being carried downstream. Midge larvae are also common in swift water, as is the water penny—the larva of a small beetle, which is so flattened that it is able to cling, as does a limpet, to the undersurface of rocks.

Since traveling in fast water is perilous, it is not surprising that some swift-water animals have come to exist by means of devices which enable them to catch their food as it goes by. An example of such an animal is the larva of *Hydropsyche*, a net-spinning caddis fly. Its silken basket is arranged to catch plankton drifting with the current. Other caddis flies live in cases which they have fashioned from bits of stones or debris (Fig. 7-29); they also feed on plankton. Certain snails, limpets, and crayfish are among the larger invertebrates of this community, while flatworms and larvae of such insects as May flies, stone flies, dragonflies, and damsel flies also make the stony habitat of the bottom their home.

Since plant food is largely restricted to small algae and phytoplankton, it is not surprising that detritus feeders and predators are common among the animals present. Thus Chapman and Demory (1963) found that algae feeders included certain stone flies, caddis flies, and beetle larvae.



Minnie B. Scotland

Fig. 7-29 Two caddis flies, *Agraylea multipunctata*, in their cases. Larvae of this order are aquatic, and many are adapted to life in swift water.

Detritus feeders were found among some species of immature May flies, stone flies, caddis flies, and flies. Certain stone fly and caddis fly nymphs were found to be carnivores. Some, like May fly nymphs may be algae feeders one season, detritus feeders another.

A few species of fish are able to survive the rigors of the swift-water community. Trout and such smaller fishes as the daces, shiners, and minnows live in this habitat. These fishes usually spend most of their time behind rocks and dart for the shelter of other rocks when they move, not maintaining a position in the current for any length of time. Several swift-water forms like the long-nosed dace have terete bodies, while the stone roller minnow is rather unusual in having a lower lip specially reinforced with cartilage, which it uses for scraping algae off rocks. In some of these species the swim bladder is reduced or nonfunctional, enabling the organisms to stay on the bottom of the stream.

In a study of Kentucky streams, Kuehne (1962) found that certain fish were characteristic of different-sized streams and proposed a scheme of classification that should help in comparing studies of streams throughout the country. Thus, in the headwaters (first-order streams) he studied, creek chubs were the only fish present. In second-order streams (formed by the union of two first-order streams) creek chubs dominated but now arrow darters and stone rollers were common. Third-order streams (formed by the union of two second-order streams) were dominated by these same fish, but other species also appeared. In fourth-order streams (formed by the union of two third-order streams) creek chubs and arrow darters became uncommon or rare, and seven other species appeared for the first time. Similar differences in the benthos of streams of different sizes was found by Gersbacher (1937). In this study of Illinois streams, headwater invertebrates were dominated by *Chironomus* (a bloodworm), large creeks or small rivers by *Musculium* (a clam) and *Lampsilis* (a snail), and large rivers by *Hexagenia* (a May fly), *Chironomus*, and *Viviparus* (a snail).

Higher vertebrates are not numerous in swift streams. Worthy of mention are a few salamanders which may be found under the rocks in swift water. These include the dusky salamander (*Desmognathus fuscus*), purple salamander (*Gyrinophilus porphyriticus*), and two-lined salamander (*Eurycea bislineata*). The beautifully adapted water shrew (*Sorex *palustris*) is an excellent swimmer and has fringes of hair along its feet which permit it to walk upon the surface of the water. It is found along small swift streams in wooded areas. Mink, raccoons, and other predators may feed along the edge of the stream but are not properly part of the stream community itself, in spite of their undoubtedly important effect upon it.

Although a relatively small number of species of organisms are able to live in the swift-stream community, the number of individuals may be very great. Thousands of invertebrates, of several phyla, can exist on a single rock, not to mention the bacteria and protozoa and other phytoplankton and zooplankton which exist around it. A single sweep of a seine may bring up a hundred small fishes. What is lacking in variation is made up for in numbers.

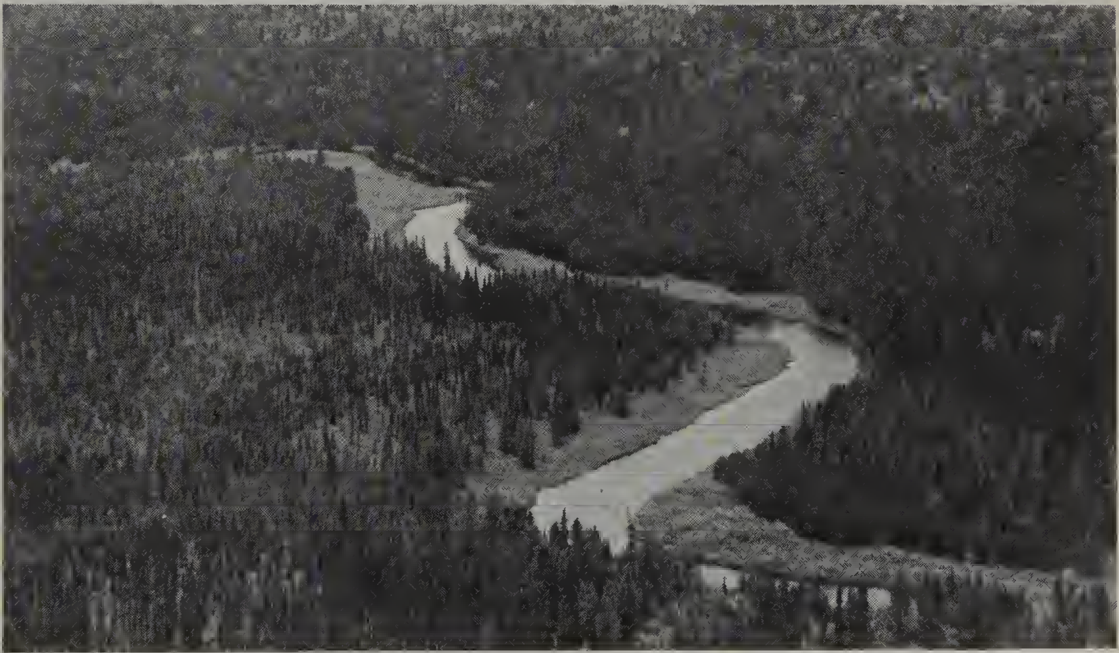
In swift streams, both flooding and droughts may kill whole populations. In floods, animals are killed as they are dashed about or are left stranded as flood waters recede. In an intermittent stream in Arizona, John (1964) found that the young of the year of the only species of fish present (*Rhinichthys osculus*) were especially vulnerable to flash floods, but older fish were most affected by the starvation occurring in overcrowded pools that remained during droughts.

Repopulation of small streams after floods or droughts is relatively rapid. Some parts of these streams may not be as severely affected by floods as others because of topography and may thus serve as population reservoirs. Adult insects may fly in or move up from downstream. In a study of drought in the headwaters of an Illinois stream, Larimore et al. (1959) found that in only two weeks 21 of 29 regularly occurring species of fish had reoccupied the stream as they moved up from downstream populations.

Pools are also important in providing refuge for organisms during droughts, from which repopulation may occur. Pools further act as nesting and nursery grounds for some fish and provide conditions suitable for survival of larger fish (Lagler et al., 1962). Populations of riffles are greater in numbers than those in pools while the stream is flowing, but other than this, the difference in fauna of riffles and pools in one section of the stream is not great (Stehr and Branson, 1938). As Kuehne (1962) points out, a greater difference occurs between the populations of upstream and downstream riffles. Riffles may act as boundaries for local populations of fish in the deeper sections of the stream, at least for fish which exhibit territorialism, such as certain suckers, sunfish, and bass (Gerking, 1953). Riffles are also important as spawning grounds where some species of fish (certain trout, darters, minnows, suckers) may bury eggs and as a habitat for aquatic insect larvae and other invertebrates such as crayfish.

Physical Conditions of Slow Streams

Where the elevation gradient is less, the stream will be slower. Usually such a slow stream will be deep and muddy-bottomed, located in a wide valley carved out by the stream itself (Fig. 7-30). The rate of flow and depth may still vary and be exceptionally great in rainy seasons. Flooding into its floodplain is a common occurrence. The lack of a strong current has its effect on other physical factors and ultimately on the type of community living in this habitat. Since it takes a strong current to move large rocks, few will be found, and silt or sand may form the bottom sediment. Near the shore and in shallow water where rooted vegetation grows, there may be accumulations of organic matter, which combine with the silt to form deep muck. Water temperature in slow streams is usually higher than that of swift streams, although deep-bottom waters may be cool. There is less chance for



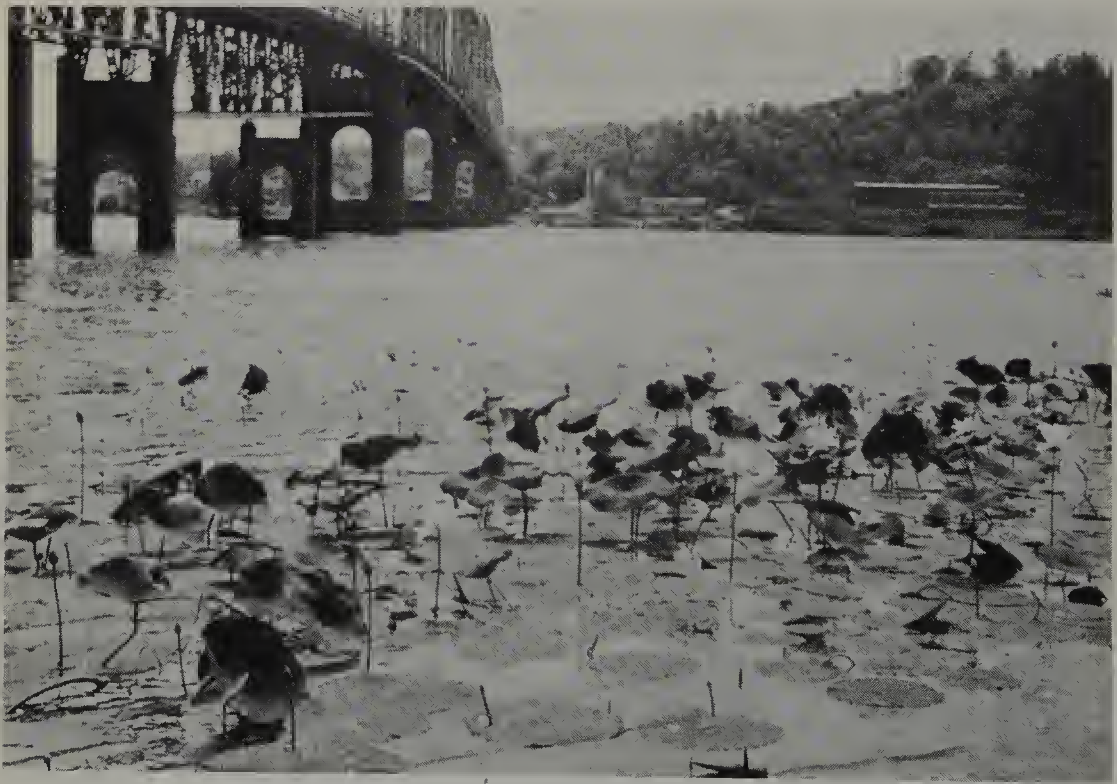
Ralph S. Palmer

Fig. 7-30 A slow meandering stream in a wide valley. Piscataquis County, Maine.

aeration of the water here than in a fast stream, so that oxygen content will be lower and carbon dioxide content higher. The water will usually be turbid. In a study of the lower Missouri River, in fact, Berner (1951) found that turbidity of the water was an all-important feature of the river, affecting almost every other characteristic.

The Life of Slow Streams

Since in still water there is no problem of maintaining position, plants are nearly always to be found along the shores of slow streams, and sometimes rooted aquatic plants such as *Potamogeton* may extend out into the center of a shallow stream. In backwaters, and sometimes along the shores, there may be the same zonation of communities found in lakes (Fig. 7-31). Plankton is also different in the slow stream. In addition to the desmids, diatoms, and other small forms of algae found in swift streams, protozoa and rotifers abound. In some rivers, plankton increases in numbers as the stream



William E. Werner, Jr.

Fig. 7-31 Aquatic vegetation zones in a backwater of a river show marked similarities to the same communities in lakes (cf. Fig. 7-14). Mississippi River at Hannibal, Missouri.

progresses from its headwaters, reaches a maximum, and then declines near the mouth of the river (Welch, 1952). Part of the decline may be due to the effects of the rooted aquatic vegetation, which acts as a strainer to prevent the further movement of the plankton downstream.

In slow streams as well as swift, there is usually a considerable population of drifting organisms. Thus Berner (1951) found an average of 0.07 pounds per surface acre in the relatively unproductive Missouri. Waters (1961) believes that a measurement of drift organisms may be used as an index of productivity of stream benthos, since such organisms represent the surplus of populations that have lost out in competition for space and other requirements.

Various factors may affect plankton productivity in large streams. In the lower Missouri River, plankton populations are very low, mainly as a result of the high turbidity (Berner, 1951). Also important is the low concentration of oxygen (less than 50 per cent saturation in midsummer). In the Sacramento River, California, plankton increases progressively downstream. In this case, water temperature was the most important factor affecting plankton populations, although current and oxygen concentrations were also important (Greenberg, 1964).

Animals of the slow stream are more varied than is the case in swift water, and include greater numbers of large species. Yet the bottom fauna may not be more numerous; for without stones, suitable dwelling places, except for burrowing animals, are lacking. Snails, clams, bryozoans, amphipods, leeches, crayfish, and earthworms may be included in the fauna. Many insect larvae and adults, similar to those of littoral communities of lakes and ponds, will be present. Vertebrates are more plentiful as well as more varied. Usually fish species which occur in fast waters are not found in slow streams, perhaps because of their oxygen or temperature requirements. Some require particular conditions for parts of their life cycle, such as a certain type of bottom for spawning. Silt covering the bottom rubble may prevent successful breeding by certain fast-water forms. In the larger rivers, gill-breathing salamanders like the mud puppy, *Necturus,* and large turtles like the snapper, *Chelydra,* are frequently present.

The Upstream Movement of Succession

As the headwaters of a stream wear the hills down, more and more of the stream will have a slow current, and so succession moves upstream. The slow-water community invades and replaces the swift-water community. If we travel the length of a stream, we may observe a gradual change in biota as the shift from slow to swift water takes place. There will be irregularities in the transition, for rapids will be interrupted by pools, and these pools may possess some species belonging to the slow-water community. Furthermore, the current is not uniform across a stream, nor from the surface to the bottom, and these variations will produce deviations in the community. In general, however, the sere is clearly recognizable and demonstrates a kind of succession.

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chapter 8

The marine environment

The study of the oceans is called oceanography. This science is a very broad one and consists of several major divisions: physical oceanography, which deals with currents, waves, tides, density, conductivity, transparency, and other properties of sea water; geological oceanography, which includes the study of the formation of the ocean floor, sedimentation, bottom topography, and erosion; chemical oceanography, which is concerned with the constituents of the salts in the oceans, the elements, and organic and inorganic compounds in the oceans; and biological oceanography, which deals with all aspects of life in the sea. Very often studies in one of these divisions require knowledge of the others, especially in geological and biological oceanography. Some studies are restricted primarily to the open oceans, while others are concerned primarily with coastal waters. On the other hand, all aspects of the oceans may be of significance to any other one.

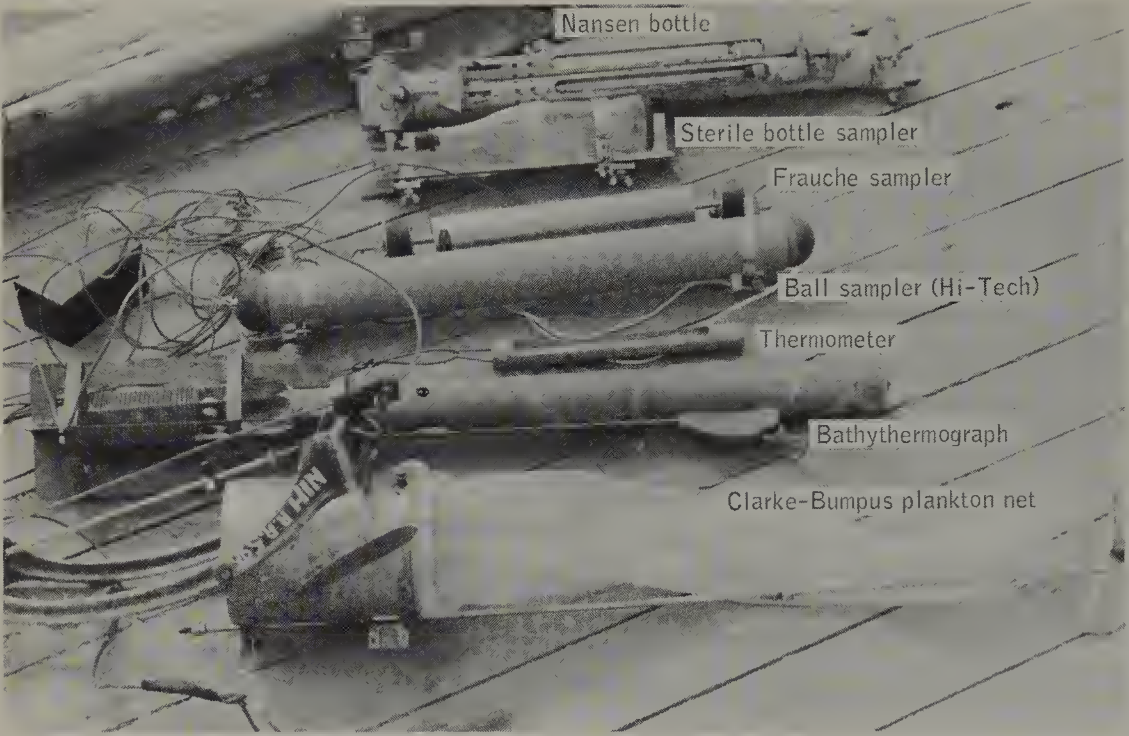
The study of the open oceans has, until recent times, been

Beneath the waves there are many dominions yet to be visited and kingdoms to be discovered, and he who venturously brings up from the abyss enough of their inhabitants to display the physiognomy of the country, will taste that cup of delight, the sweetness of whose draught only those who have made a discovery know.

Edward Forbes, "Natural History of European Seas," 1859

rather limited. Most of the biological work was taxonomic, a necessary first step to find out what organisms exist in the sea, and where. More recently there has been a surge in oceanographic work, some of it being carried on in land-based laboratories, and some of it on board oceanographic vessels.

Many studies can be made only on the oceans. For example, the research dealing with ocean currents, their paths, temperatures, salinity, and other properties must be made at sea. Organisms brought up from the ocean depths must often be studied in the living condition on the spot. Research conducted under these circumstances is expensive, and this fact is probably one of the reasons for the paucity of our knowledge of the oceans, for only governments and modern-day foundations are wealthy enough to support research requiring oceanic vessels. Dupree (1959) gives an interesting account of the difficulties of obtaining financial support for oceanic expeditions a century ago. Today, governments are more



William E. Werner, Jr.

(*a*) Sampling devices (from top to bottom): a Nansen bottle with reversing thermometer, a sterile bottle sampler, a Frauche sampler, a Hi-Tech Ball sampler, a thermometer, a bathythermograph which makes continuous recordings of temperature as it is lowered, and a Clark-Bumpus plankton net.

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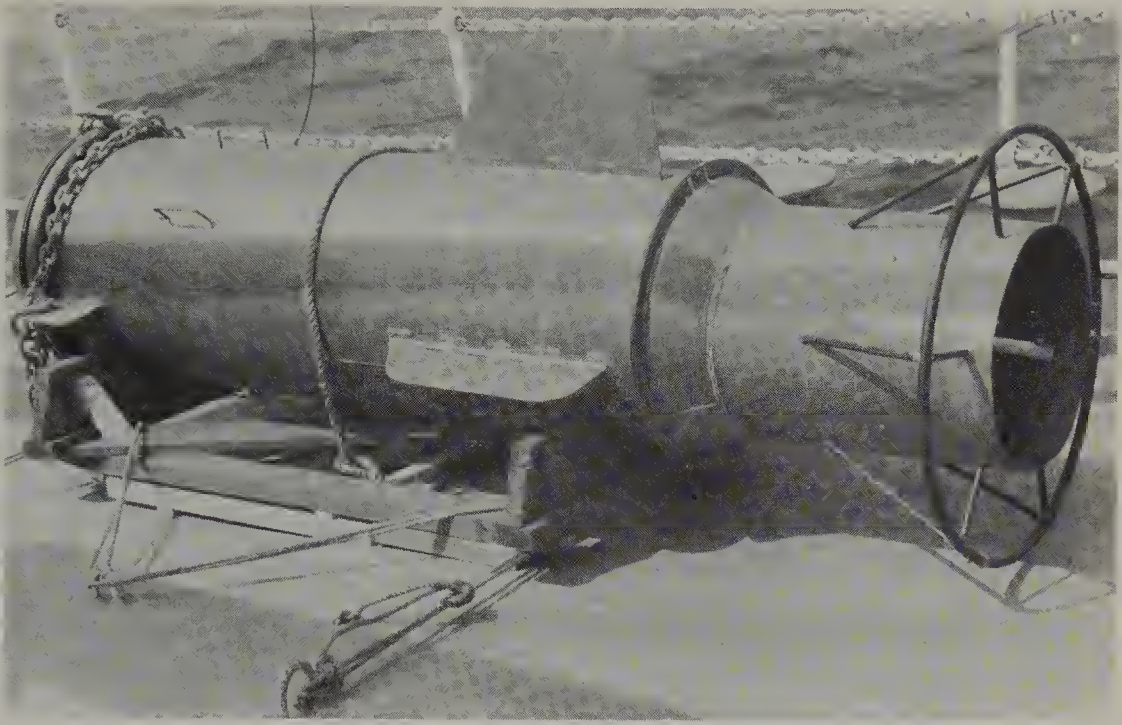
(*b*) A Van Veen grab, capable of taking a bottom sample of approximately ⅕ square meter.



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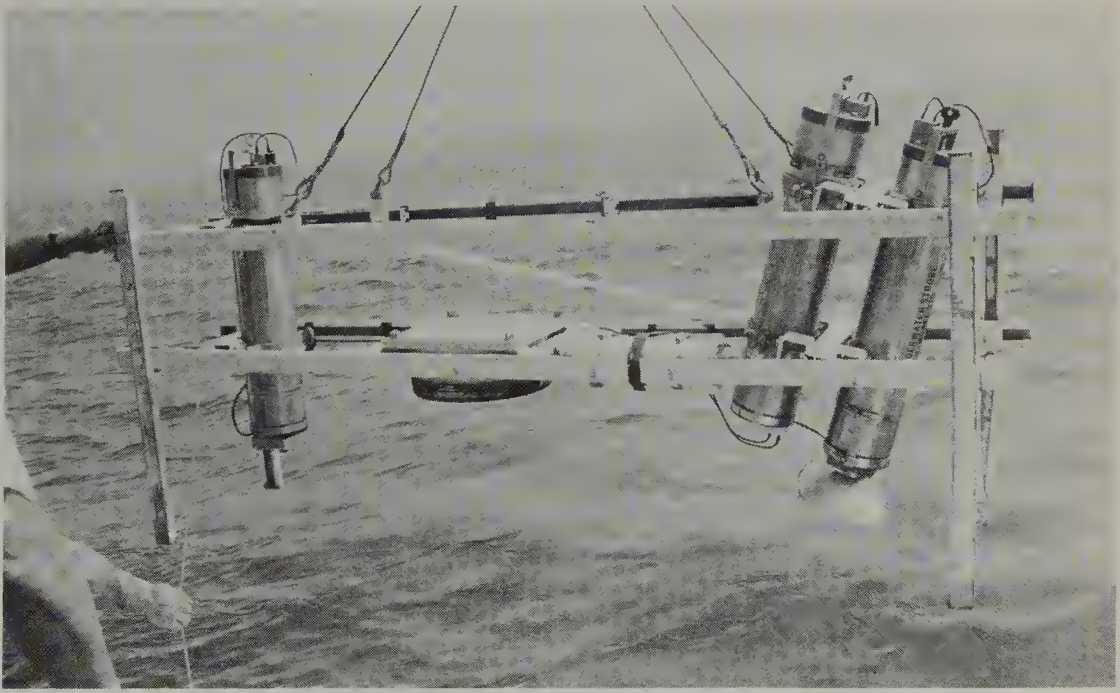
(*c*) The housing for a large high-speed plankton net.



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(*d*) An Edgerton camera for photographing the bottom. A strobe light flashes and a picture is taken simultaneously at 12-second intervals. A "pinger" on the device allows the operator to determine when the camera is near the bottom.

Fig. 8-1 Some oceanographic equipment.

interested in supporting oceanic research since its economic importance has been demonstrated.

Another reason for the more recent surge of research in oceanography is the development of suitable equipment and techniques. Magellan used a cannon ball on a rope in an unsuccessful attempt to plumb the depth of the ocean, whereas today research vessels use electronic sonar devices which make a continuous record of the depth of the ocean under the ship. Expeditions until the late nineteenth century used rope to lower dredges or other sampling devices. Even the famous Challenger Expedition of 1873–1876 used rope, although wire was tried. Today, steel cables and power-driven winches lower and raise water-sample bottles, plankton nets, trawls, dredges, coring devices, and photographic equipment (Fig. 8-1).

The vastness of the oceans is another reason for the spottiness of our knowledge of the sea. The surface area of the oceans is over 126 million square miles or approximately 71 per cent of the earth's surface. Its depths (such as the Mindinao Trench, 37,782 feet) are greater than the elevations of the highest mountains, and the average depth is approximately 5 times the average height of land. One of the difficulties posed by oceanic exploration, then, is the vastness of the seas compared with the puny-sized samples oceanographers are able to take. Collecting devices cannot be large because of the size and weight of the cable that would be required to lower big samplers to great depths. Even with modern power winches, it may take several hours to lower a net to the bottom and several more to raise it. Currents and movements of the vessel may foul the gear, so that nets may come up empty or filled with unwanted bottom debris. Diving suits allow a man to descend to a maximum of about 535 feet. The bathyscaph *Trieste* has descended to over 35,000 feet (Piccard, 1960), and from it one may observe organisms and photograph them, make temperature and current recordings, and even pick up some objects. However, our knowledge of life on the ocean bottoms and at great depths is still meager. For example, it was not until the Galathea Expedition of 1950–1952 that it was ascertained that there was abundant life at great depths.

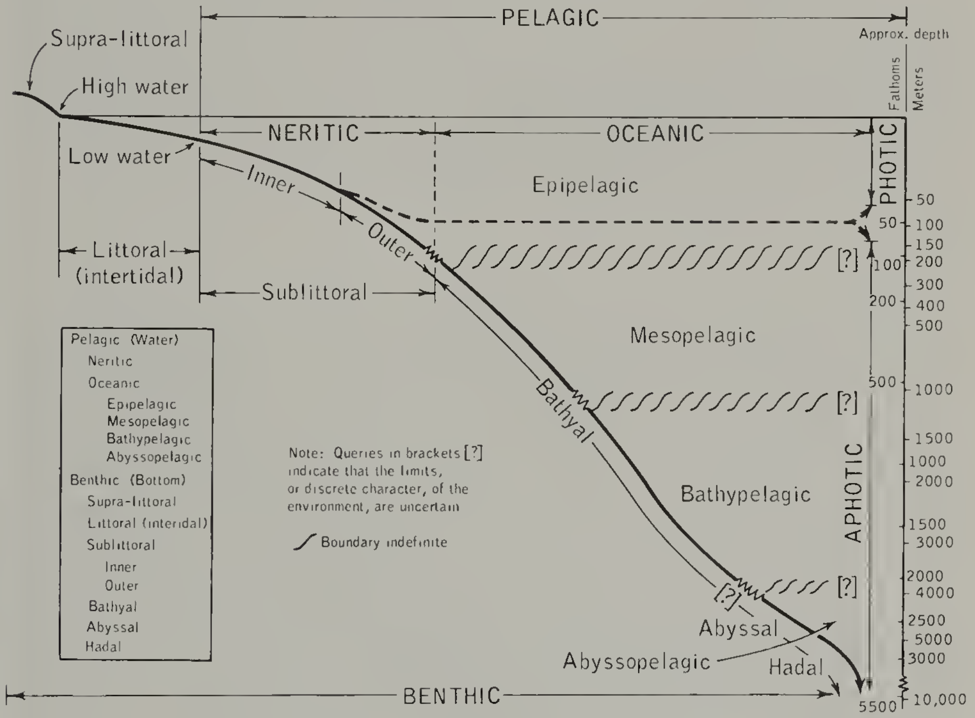
One difficulty of ocean studies in the past has been that one vessel working in one part of the ocean could obtain data from only a very limited area of the ocean at any one time. Recently, the Indian Ocean Expedition of 1961–1963 was conducted, in which 40 ships of 25 nations participated. Meanwhile, the equatorial Atlantic Ocean is being studied by vessels of eight nations in projects called Equilant I and II. The data from all ships are processed and sent to all participating nations. From such research, man is gradually piecing together a total picture of the physical, chemical, geological, and biological conditions of the oceans.

CLASSIFICATION OF MARINE ENVIRONMENTS AND COMMUNITIES

The classification of marine environments proposed by Hedgpeth (1957*b*) has gained considerable acceptance (Fig. 8-2). According to this scheme, there are two major environments in the sea, *benthic* (bottom) and *pelagic* (open sea).

Benthic Environments

The uppermost of the benthic habitats is the supralittoral zone, which is the beach down to the edge of the sea. Where there are tides, the lower boundary of the supralittoral is the



Note: Queries in brackets [?] indicate that the limits, or discrete character, of the environment, are uncertain

Fig. 8-2 A classification of marine environments. From Hedgpeth, J. W. 1957. In "Treatise of Limnology and Paleoecology, Vol. I, Ecology." *Geol. Soc. Am. Mem.* 67. New York, pp. 17–27.

high-tide mark. The littoral zone is the area between upper and lower tide levels and is therefore called the intertidal level by some. It is the margin of the sea. The sublittoral zone extends from the lower limit of the littoral to the edge of the continental shelf. The sublittoral is divided into the inner and outer sublittoral. The inner sublittoral is distinguished from the outer by the presence of attached algae in the former, the latter being too deep (50 to 200 meters) for effective photosynthesis. The *bathyal* zone occurs on the continental slope, where the bottom of the ocean descends rapidly from about 200 meters down to 3,000 or 4,000 meters. From this depth to approximately 6,000 meters is the *abyssal* region, in which the temperature is never above 4° Centigrade. In the great trenches of the ocean, where depths may be as great as 10,000 meters, the benthic zone is called *hadal*, since preliminary investigations indicate the fauna here is quite different from that of the abyssal zone (Hedgpeth, 1957*b*).

Pelagic Environments

The open sea above the benthic region is the other general environment and is known as the pelagic. The water over the continental shelf is that part of the pelagic known as the *neritic* zone, while the water over the continental slope and the greater ocean depths is called the *oceanic* zone. This in turn is divided into several subzones (*epipelagic, mesopelagic, bathypelagic*) according to various depths (Fig. 8-2).

Marine Communities

Agreement on a classification of marine communities is even more difficult than for a classification of environments. Several workers have used the term biome in describing littoral communities (Marshall, 1953; Shelford et al., 1935; and others). Allee et al. (1949) point out that according to certain criteria for biomes, there should be only two or possibly three marine biomes—benthic, pelagic, and possibly coral reefs, which they call biome-like. Kendeigh (1961) recognizes four biomes—pelagic, rocky shores, muddy and sandy beaches, and coral reefs and atolls. However, as Odum (1959) points out, benthic organisms are really a part of zonal communities, not major communities in themselves. In other words, pelagic and benthic organisms at a given depth are part of the same communities. Hedgpeth (1957*a*) points out that phenomena on land and in the oceans are not the same. Thus, although a kind of succession does occur (Hewatt, 1935; Reish, 1961; Shelford et al., 1935), it is quite different from terrestrial succession, and the concept of climax fits even less well. The factors determining the equilibrium of a marine community are primarily physical. It would seem best, at least at this stage of our knowledge of marine communities, if the terms applied to larger terrestrial communities, such as biomes and climax, are not applied to marine situations.

GENERAL FEATURES OF NORTH AMERICAN COASTS

Currents

The shores of the East coast exhibit several differences from those of the West coast, although there are of course many similarities too. Among the most important reasons for differences are the oceanic currents along each shore. The following description of surface water movements is extremely simplified and generalized, but for the purposes of this discussion brings out certain situations of significance. For detailed information on currents, see Sverdrup et al. (1942).

For various reasons, the general path of movement of the upper oceanic water on the East coast is toward the northeast. The warm current known as the Gulf Stream moves up from the Caribbean. A part of it, called the Florida Current, comes close to the shore off Florida. The Gulf Stream continues north along the coast and is met by the cold Labrador Current moving south from the arctic. These currents merge and move across the Atlantic as the North Atlantic Current. Eventually the current moves south along the western coast of Europe to the equator and then across the Atlantic as the North Equatorial Current, where it is warmed. It now moves once again up to the Caribbean. One part travels past the Yucatan Peninsula and into the Gulf of Mexico, then rejoins the remainder of the stream which has flowed to the east of the Caribbean. Water from the Southern Hemisphere also joins the stream in the Caribbean (Fig. 8-3*a*).

In the Pacific, the Kuroshio Current and its extension, the North Pacific Current, join the cold Subarctic Current below Alaska. Now called the California Current, it moves down the coast off Washington, Oregon, and California to Baja California, then turns west above the equator as the Pacific North Equatorial Current. Finally, the current, now warmed, turns

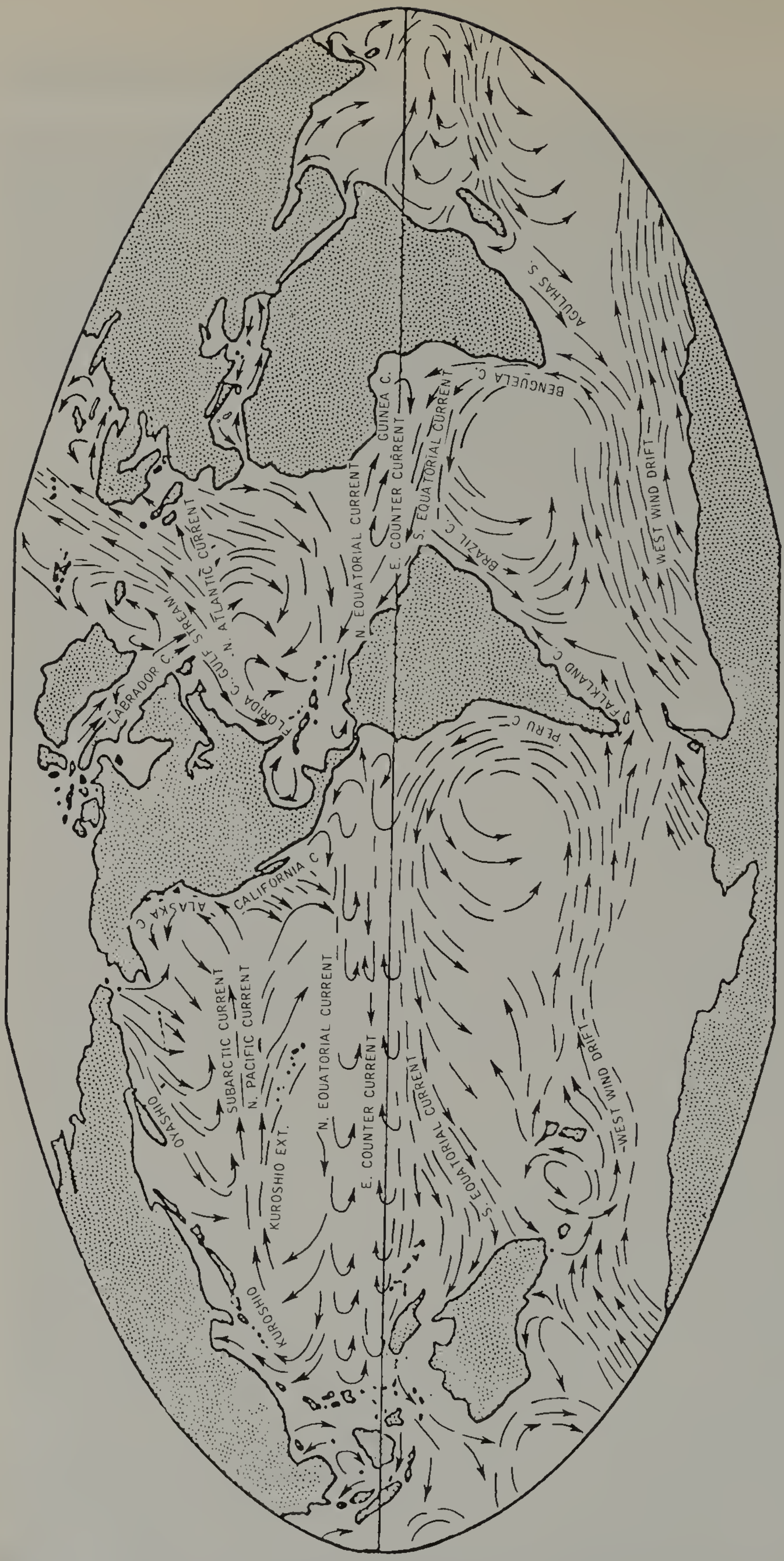
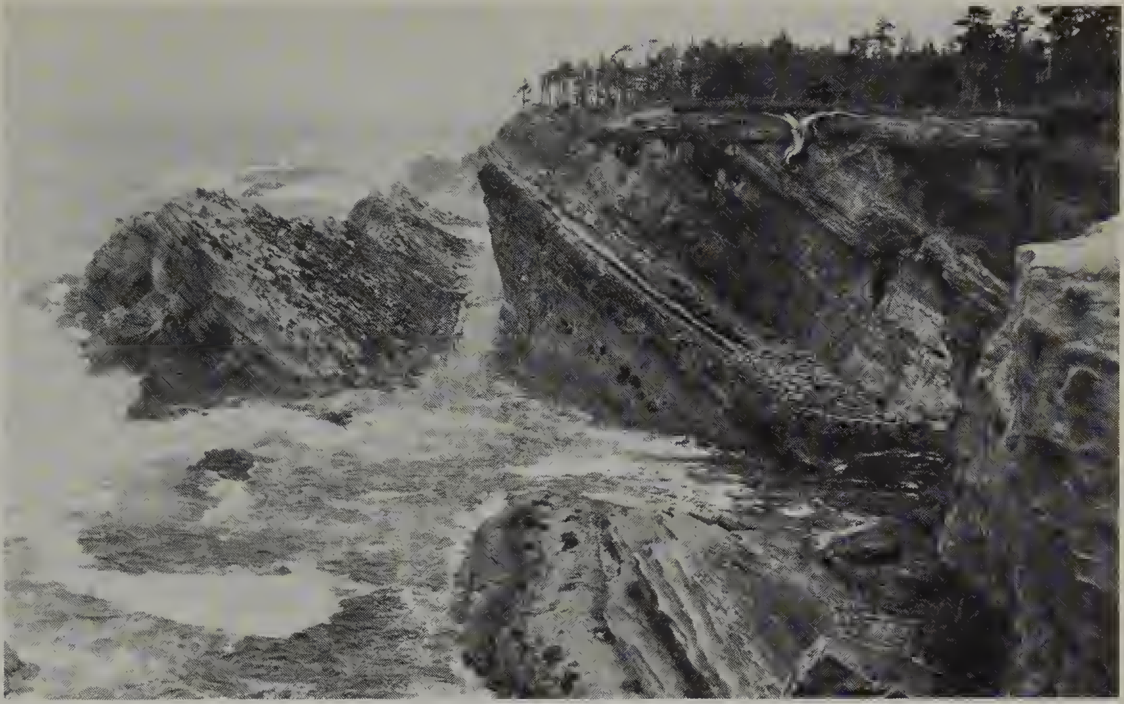


Fig. 8-3*a* Surface currents of the ocean in February-March. Data from Sverdrup et al., 1942, by permission of the publisher.



Allan G. Heath

Fig. 8-3*b* The surf along the Oregon coast. On exposed coasts, it is extremely dangerous to wade in the littoral zone because of the strength of the surf action and occasional high swells.

mostly north and flows on past Formosa and Japan, where it becomes once again the Kuroshio Current.

Thus on the East coast the currents flowing near the coast are warm, having come recently from equatorial locations, while the currents off the West coast are cold, having been chilled by arctic waters. Furthermore, upwelling of cold bottom waters along the Pacific coast tends to keep the coast cooler at much lower latitudes than one would ordinarily expect (Sverdrup et al., 1942).

Wave Shock

Another condition of importance to organisms is wave shock, which also differs on the two coasts. Because of the prevailing westerly direction of the winds and the absence of protecting coastal islands, the ground swells are much greater on the Pacific coast than on the Atlantic coast of North America (Fig. 8-3*b*). This results in much heavier surf and greater wave shock on the West coast than is generally found on the East coast (Ricketts and Calvin, 1952).

Dispersal Barriers

The union of the Labrador Current with the Gulf Stream occurs in part off Cape Cod, Massachusetts, creating a relatively sudden change in temperature of the ocean water. This presents a barrier across which many (but not all) marine species cannot pass, either from north to south or south to north, because they cannot tolerate the temperatures encountered beyond this point. Other dispersal barriers are said to exist at Newfoundland; Cape Hatteras, North Carolina; and Cape Kennedy, Florida, where there are critical changes in the ocean temperatures (Fig. 8-4). On the Pacific coast, temperature gradients are much more gradual, resulting in broad transitional zones rather than sharp dispersal barriers.

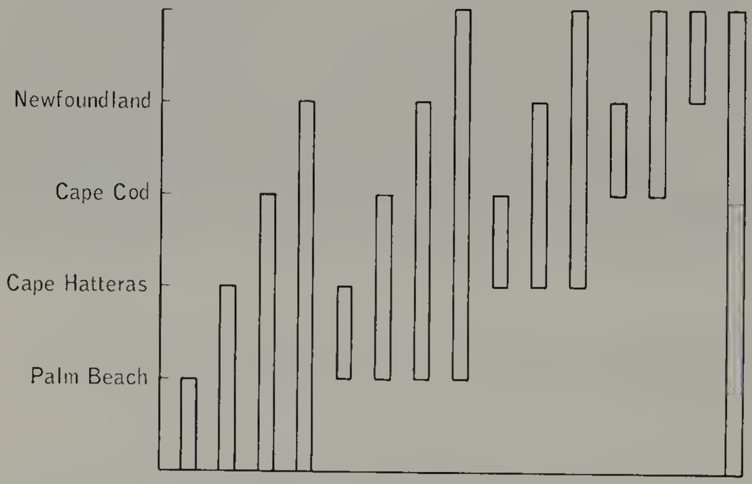


Fig. 8-4 Schematic representation of the components of the American coast biota, with reference to the important change-points of Newfoundland, Cape Cod, Cape Hatteras, and Palm Beach (Cape Kennedy). Fifteen possible ranges exist, of which fourteen are zonal and one is ubiquitous. From Hutchins, Louis W. 1947. The bases for temperature zonation in geographical distribution. *Ecol. Monographs*, 17:325–335.

It should be observed that the temperature tolerances which may limit a species' distribution may be more critical at one part of its life cycle than another. Hutchins (1947) devised a rule for the effects of temperature on the dispersal of various species, which states that the poleward limits for some species are determined by minimum temperatures. Some species reach a limit in poleward dispersal because the water is not warm enough in summer for breeding. Other species are stopped from further poleward dispersal because they reach a point where winter temperatures are too low for survival. Conversely, some species are limited equatorward by their inability to survive high summer temperatures, and others are limited in equatorward distribution by reaching the point where even winter temperatures are too warm for reproduction. Since these poleward and equatorward distribution requirements may be found in various combinations for any one species, there are four zonal types with respect to restriction of dispersal by temperature (Fig. 8-5*a*, *b*). Exceptions to this example of restriction of dispersal include situations in which the animal may be present in an area but does not complete its life cycle there. Also, each stage of the life cycle of an animal may be differently restricted in dispersal by temperature and other factors.

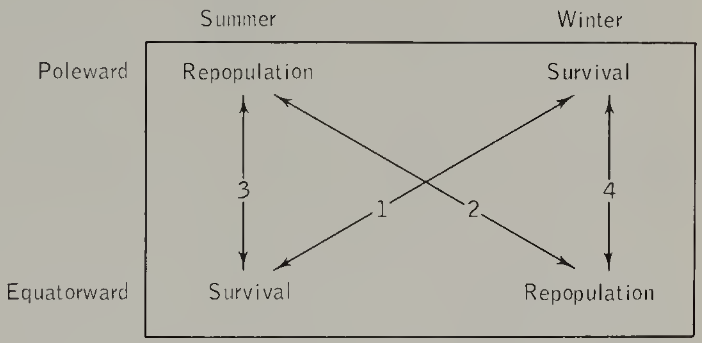


Fig. 8-5*a* Diagram of the four basic types of zonation, showing for each the season providing the critical poleward and equatorward conditions. The terms inside the box suggest the usual sort of relationships involved—i.e., survival tolerance of the most resistant stage, or the requirements for some phase of repopulation. From Hutchins, Louis W. 1947. The bases for temperature zonation in geographical distribution. *Ecol. Monographs*, 17:325–335.

Estuaries

Along the coasts there are, of course, the outlets of rivers and streams, and these create habitats called estuaries. An estuary may be defined as an inlet of the ocean where there is a mixture of fresh and salt water, or that part of a river emptying into the ocean which exhibits tidal phenomena. The water involved normally has a free connection with the ocean, allowing circulation of water and other substances. Examples of estuaries include the lower Hudson River, Chesapeake Bay, and the mouth of the Mississippi River, as well as the mouths

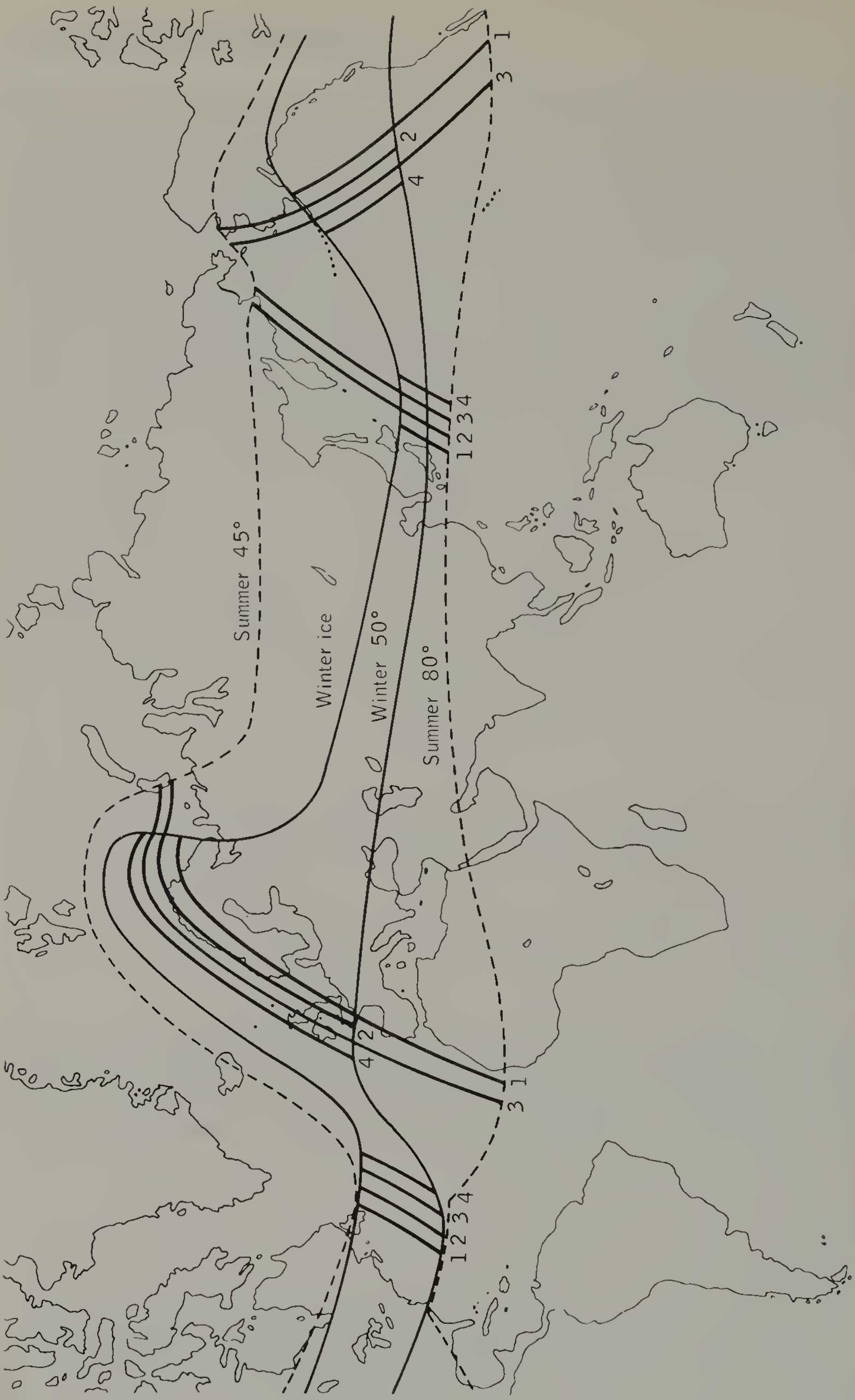


Fig. 8-5*b* Diagram showing the geographical extent on the major coasts of zones of the four types, using as limiting intensities monthly mean temperatures of surface water at Newfoundland and Cape Hatteras. The four types of zones are coextensive on the American Atlantic coast, but have independent, distinctive patterns of occurrence on other coasts. From Hutchins, *op. cit.*

of many other rivers emptying into the Atlantic and Pacific Oceans.

The physical aspects of estuaries differ according to several variables, including the width of the mouth of the river, volume of fresh water emptying into the ocean, extent of tidal fluctuations of the area, oceanic currents, and relative temperature of the sea water and fresh water. One of the most important features of an estuary is that it is a region of gradual dilution of salt water, becoming progressively fresh upstream. The exact pattern of dilution is complex because of the difference in density of salt and fresh water, variability of current from one part of the estuary to another, and change in rate of flow with the tidal sequence. Salt water is normally heavier than fresh (unless the sea water is warm and the fresh water is very cold), so it often flows upstream on the bottom, mixes with fresh water, and flows out to sea diluted. However, the exact pattern of the mixing depends upon the particular estuary (Emery et al., 1957). In general, one can only say that dilution does gradually occur, and organisms must be able to tolerate variations in salinity in order to penetrate estuaries to any great distance.

Another factor of significance in estuaries is sedimentation. As rivers meet the sea, their load of sediment is dropped, in part from the slowing of the current, in part from precipitation as charged sediment particles unite with ions of the sea water. As a result, estuarian bottoms are nearly always muddy, and there are frequently deltas which are continually growing and changing the nature of the estuary.

Estuaries are highly important areas biologically. Many commercially valuable fishes and other seafood animals, such as shrimp and oysters, spend at least a part of their lives in estuaries. For some animals (e.g., shad and striped bass), estuaries are breeding grounds, while for others (e.g., shrimp), they provide a nursery ground where the young may grow to maturity before moving back to sea. Estuaries are also feeding grounds for adult fishes. Estuaries may have been important as an evolutionary pathway for development of fresh-water forms from the ocean, or vice versa, since in an estuary salinities are gradually lowered upstream. An interesting adaptation to estuarian life is indicated by the study of Pearcy and Richards (1962), who found that 97 per cent of the fish larvae collected in a New England estuary developed from eggs which sink, rather than from floating eggs. They hypothesize that this type of egg, which is larger and gives rise to a bigger and better developed larva, has an advantage in that it remains in the estuary instead of being swept out to sea, as might easily happen to floating eggs or larvae less well developed at hatching.

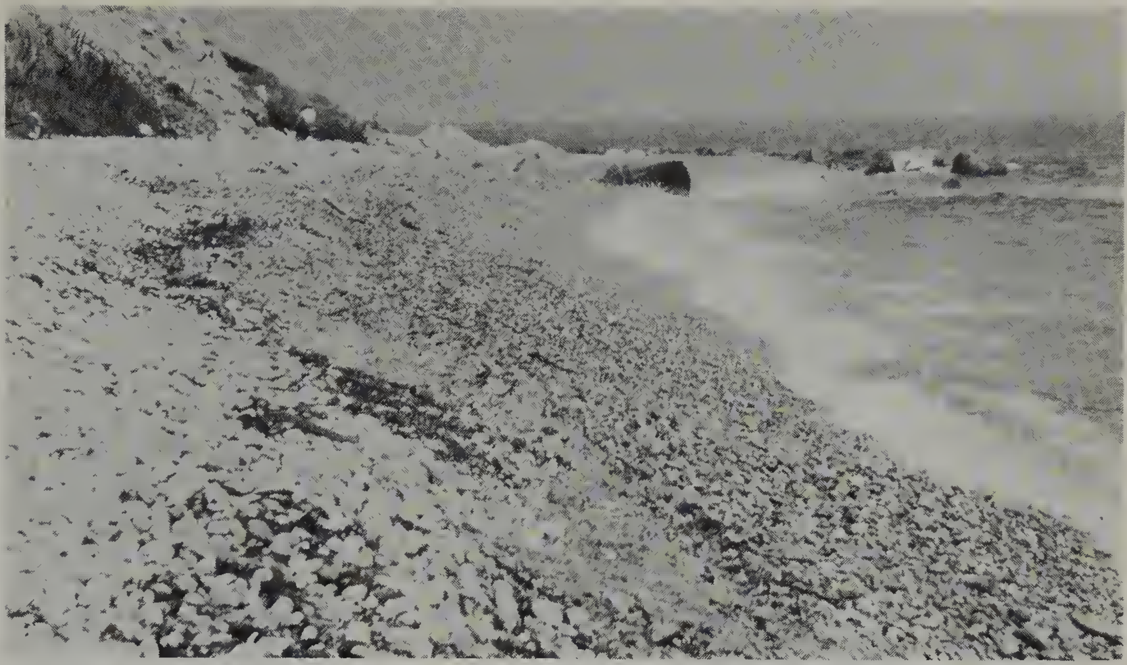
Finally, estuaries are frequently disturbed by the acts of man. Estuaries sometimes serve as the receptacle of human sewage and industrial pollution. Often jetties, bulkheads, and other artificial structures are built for navigational or recreational purposes, which usually change the environment drastically. These disturbances add to the complexity of the physical features of estuaries and consequently increase the difficulty of understanding communities of such areas. Most important of all, however, is the destruction of organisms in an area capable of producing large amounts of food.

Shore Types

The type of shore along an ocean coast is determined by various factors; these include the coastal contour, degree of exposure to wind and waves, type of substrate, and recent geology. If the shore projects out into the ocean or if prevailing winds blow directly on it, one may expect it to be exposed to currents, waves, and heavy surf. Along such shores one may find rock cliffs or rock, gravel, or sand beaches (Fig. 8-6). Sand, however, is easily moved, especially during storms, and may be an unstable feature. Rocky shores are common along the Pacific and New England coasts (Fig. 8-7*a*, *b*). Sandy beaches are relatively common along the Atlantic coast and comparatively rare on the Pacific coast.

Where the coast does not protrude or is protected from heavy wave action, a different type of shore may be expected. A slight indentation of the coast (embayment) may provide protection at least in the center of the indentation. This may allow development of sandy, or, rarely, mud beaches in the protected area, although rocky beaches may prevail at either end of the indentation.

With more complete protection, as afforded by bays, sounds, and estuaries, wave action is greatly reduced, and so mud beaches become abundant, although other kinds of beaches may develop. Often there may be strong tidal currents, especially in narrow inlets to bays. In such situations, all the water which enters or leaves the bay as the tides change must pass through a restricted passageway and so the current



William E. Werner, Jr.

Fig. 8-6 A cobblestone beach on Block Island, Rhode Island. The stones at the water level are in constant motion, making life on such a beach difficult.

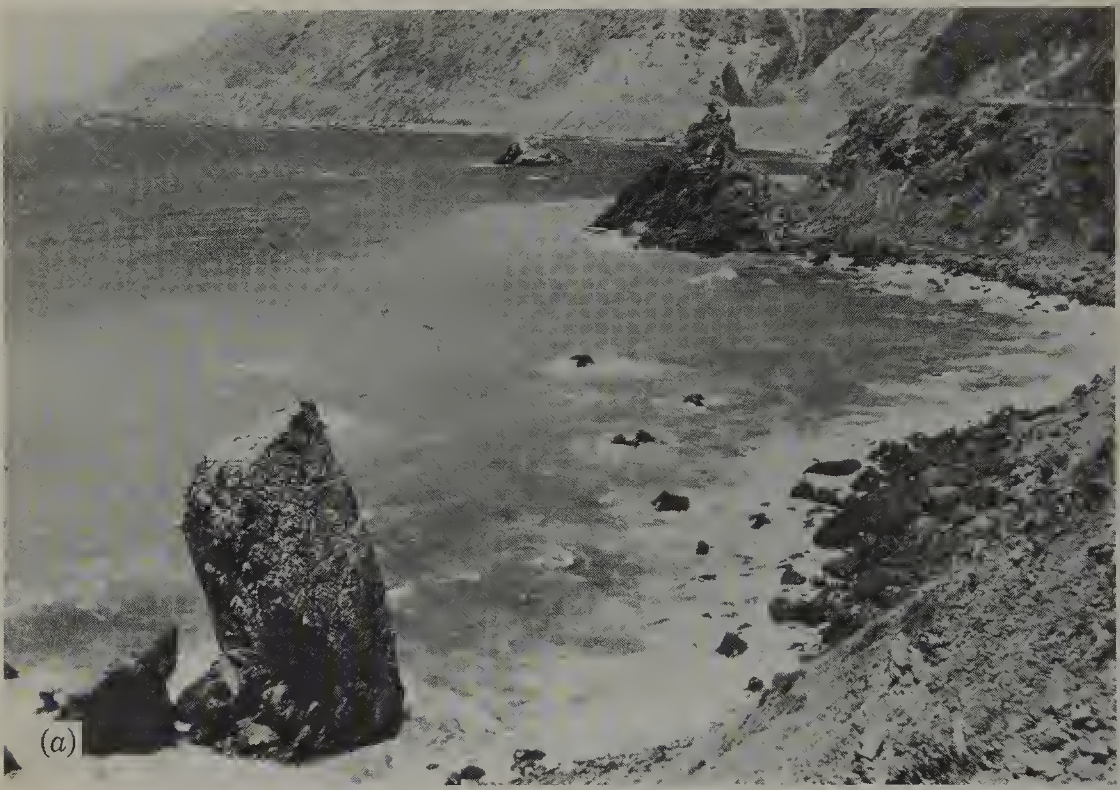
will be exceptionally swift. Sometimes, because of the structure of a bay and its inlet, the tide will suddenly enter the inlet as a wall of water several feet high (a tidal bore). The bore in the Bay of Fundy in New Brunswick, Canada, is a well-known example of the phenomenon.

PHYSICAL FEATURES OF THE LITTORAL ZONE

Tides

A dominant physical factor of most (but not all) coasts is the presence of tides. Tides may occur regularly or irregularly twice a day, or regularly or irregularly once a day, while in some places they may be lacking altogether (see map in Doty, 1957). The range of tides in various parts of the world varies from a few inches to about 50 feet.

The shores of the United States illustrate nearly all the types of tides and a considerable variety in tidal range. On the Atlantic coast, there are regular semidaily tides which range from about 6 feet in New England to 3 feet or less in Florida. Along the Gulf of Mexico, tides range from nearly



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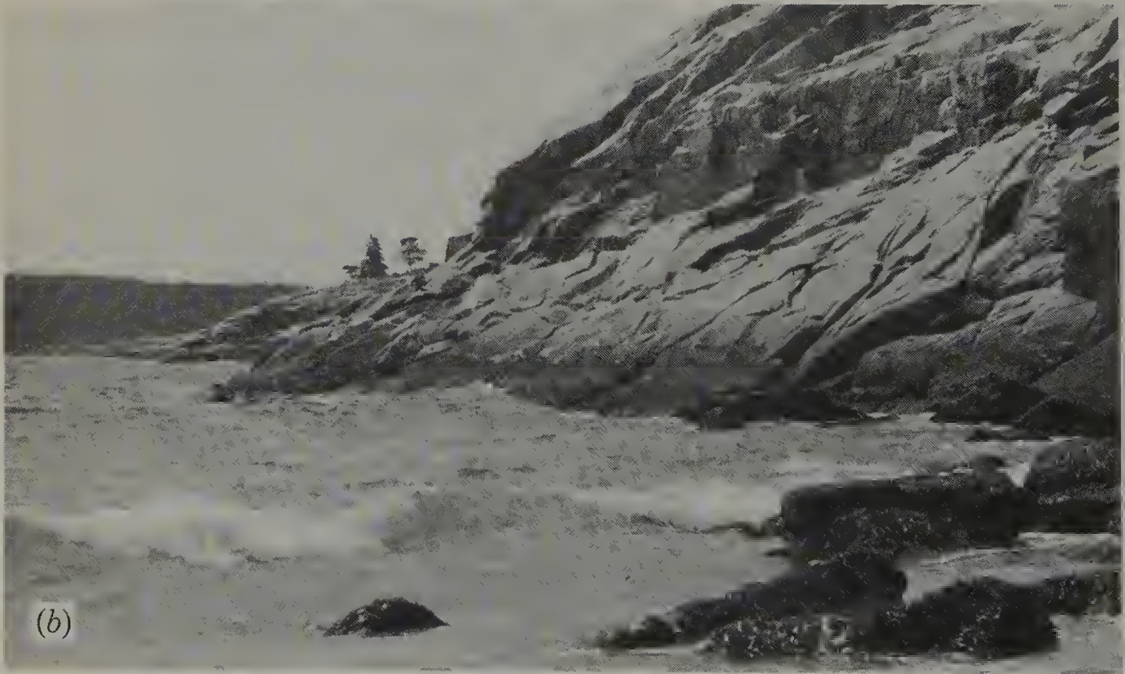
(*a*) California, south of Monterey.



Allen H. Benton

(*b*) Mount Desert Island, Maine.

Fig. 8-7 Rocky coastlines.

3 feet to about 9 feet, and at various points all four types of tides are found. On the Pacific coast, the irregular semidaily type of tide prevails; it ranges from 9 to 12 feet along much of the California, Oregon, and Washington coasts to about 24 feet on certain shores of Alaska (Doty, 1957). However, the tidal range varies with different phases of the moon; when moon and sun are in opposition or conjunction there are tides of 20 per cent greater range (spring tides), and during the quarter phases of the moon, tides of 20 per cent smaller range (neap tides). Tides vary also with the season, being of smallest amplitude in June and greatest in December. In addition, storms may cause disturbance of the tides and produce unusually high water. The tidal rhythm is variable from one location to another, especially within bays, estuaries, and other situations in which there may be an interference with tidal flow.

Substrate Movement

Tidal flow produces currents which vary according to the range of the tide, bottom topography, and other conditions. Moreover, there may be added movement of water from wind action. As water moves, it will pick up and carry particles of sediment or sand according to the degree of movement of the water. If many particles are suspended in the water, they lower the penetration of light and thus affect photosynthesis and plant productivity. In storms off Florida coasts, turbulence of the water may cause so many sand grains to be suspended in the water that they will irritate the mucous membranes of the gills of certain species of fish. The membranes are thereby stimulated to produce more mucous, which traps more sand until it fills the gill chambers. This, plus the abrasive action of the sand on the gill filaments, kills the fish (Robins, 1957). On rock coasts, heavy surf may move stones and thereby crush organisms living on the rocks. This is a major reason why there are so few organisms living on a gravel or cobble beach.

Air-Sea Interface

As the tide goes in and out, water will cover the upper limits of the littoral zone only briefly, while the lower limits will be under water for all but brief periods. Studies have also shown that the rate at which the tide ebbs and flows is not the same throughout the tidal cycle but is slowest at the extremities, that is, near the times when the tides are changing. The difference in exposure to air and to water from the upper to the lower part of the intertidal zone causes variations in the total amount of insolation, temperature, salinity, and degree of desiccation found throughout the zone. Under certain circumstances it may also cause variations in pH, and carbon dioxide and oxygen content of the water, especially in tide pools.

Light and Temperature

The lowest part of the intertidal zone will have more light absorbed by the water than will those shallower parts of the zone nearer the high-water mark. This is probably one of the factors determining the presence of algae with different pigments at various tidal levels. The part of the intertidal left uncovered the longest will also heat up the most in summer and in colder climates will become the coldest. In order to survive, organisms inhabiting this part of the intertidal zone must either move up and down with the tide, burrow, or be able to tolerate the temperature variations. Organisms which are able to withstand such wide temperature variations are called *eurythermal;* those unable to survive broad variations, *stenothermal.* In a study of rocky-shore tide pools in New Brunswick, Canada, Klugh (1924) found that temperature was the only physical factor definitely limiting organisms, although light might be for some species.

Desiccation

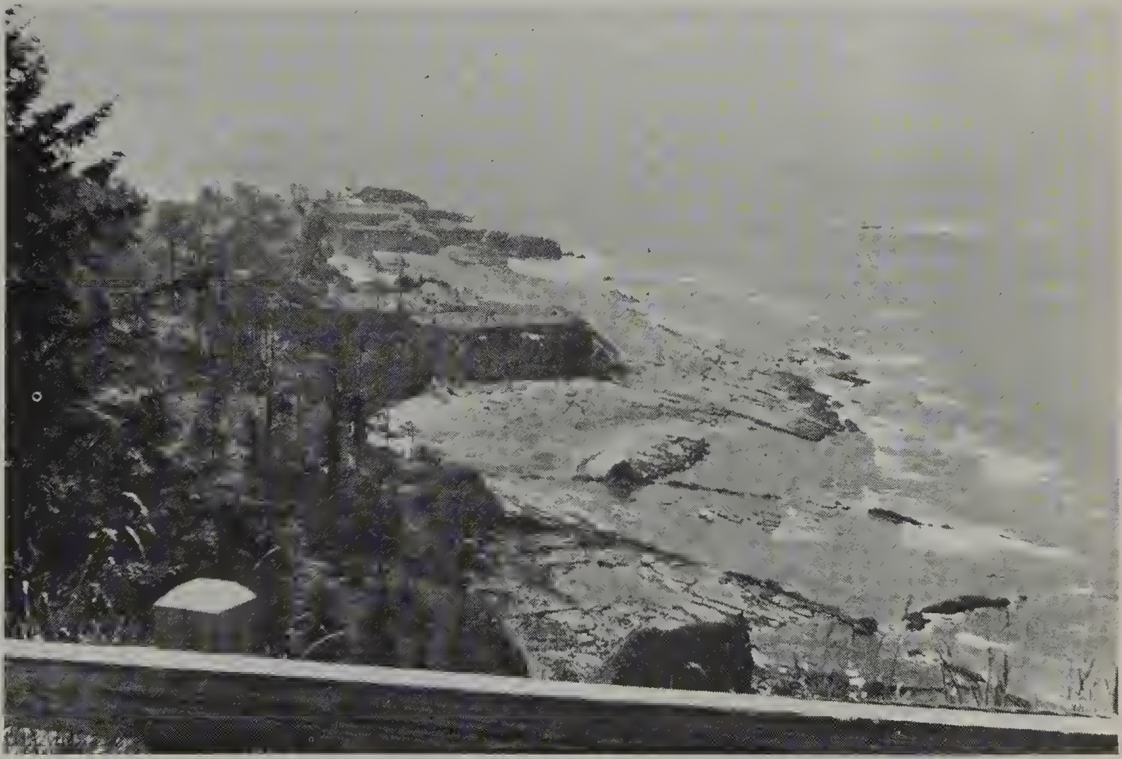
The upper part of the intertidal zone is also more subject to desiccation, or drying, although where there is a surf, splashing above the momentary level of the sea may alleviate the problem somewhat. Desiccation is a problem of significance, however, as can be demonstrated by the fact that many animals common in the upper intertidal zone have special adaptations to avoid drying out. For example, snails living in the area have tight-fitting opercula, while barnacles have snug valves and are able to keep them closed for long periods to conserve moisture inside. Crabs characteristic of the upper beaches, such as hermit crabs and ghost crabs, have special enlarged gill chambers and increased respiratory surface, allowing the chambers to act as lungs.

Salinity

Variations in salinity are important to organisms in tide pools and in some cases to organisms exposed to the air when the tide is out (Fig. 8-8). The salinity of tide pools in the upper part of the intertidal zone is subjected to greater variation than those in the lower part for two reasons. First, it is subjected to longer periods of insolation and thus to evaporation and increased salinity. Second, the upper part of the zone is more subject to dilution of sea water by rain and fresh-water seepage. Organisms which can tolerate wide fluctuations in salinity are called *euryhaline,* while those which cannot tolerate such variations are known as *stenohaline.* In the open ocean, the variation in salinity is so small as not to be biologically significant.

Dissolved Gases and pH

Although sedentary animals exposed to air when the tide is out may be affected by changes in gases and pH on their



Allan G. Heath

Fig. 8-8 A rocky beach with a broad intertidal zone and numerous tide pools. Oregon.

surfaces, these changes are probably secondary to changes in temperature and desiccation. In tide pools, desiccation is usually not a problem, although changes in salinity may affect oxygen requirements of some animals, as they expend oxygen in osmoregulation at low salinities. As the temperature of tide pools increases, dissolved gases, especially oxygen and carbon dioxide, may decrease according to physical laws. On the other hand, during the daytime, algae in these pools may produce abundant oxygen until temperatures are reached which are detrimental to photosynthesis. At the same time the plants will use more carbon dioxide than they produce in respiration, which will affect the pH. If plants are absent, the situation may be quite different, especially if animals are abundant. It is easy to see, therefore, that the amount of oxygen and carbon dioxide will vary with latitude, season, weather, time of day, and other conditions. Since carbon dioxide and pH are closely related, the pH of tide pools will also vary. Again, in the open ocean, change in pH is so minor as to be of little biological importance.

In general, we may say there is more or less of a gradient of these factors from low tide to high tide. In addition, conditions near the upper limit of the tide are usually more rigorous for marine organisms than conditions farther down the beach. As Moore (1958) points out, the length of time that organisms are exposed to unfavorable environmental conditions may be as critical to survival as the degree of change experienced. Thus marine organisms in the upper parts of the intertidal are subjected to the greatest stresses.

Zonation

Along many coasts there is a zonation of organisms; that is, a few species will predominate in a narrow horizontal band, and there may be several such bands adjacent to each other from the supratidal through the intertidal, and into the subtidal zone. Zonation is especially prominent where the coast is rocky, but it may also be obvious in other situations, such as in salt marshes and mangrove forests. It is least conspicuous on sandy or gravelly beaches. For a given geographical region and type of habitat, certain plants and animals will dominate at various levels of the supralittoral and intertidal zones, but throughout the world the species and even life forms are not always the same for a given level. For example, at the lower extremity of the intertidal zone, *Laminaria* (kelp) dominates in New England and California, but is absent in Florida. On the other hand, barnacles are present in the intertidal zone of rocky shores of these localities, although they are primarily members of different genera in Florida. Many workers have studied intertidal zonation, among them Doty (1946), Hewatt (1937), Rigg and Miller (1949), Ricketts and Calvin (1952), and Stephenson and Stephenson (1949, 1950, 1952, 1954). Doty (1957) has reviewed the world literature on the subject. There is some disagreement about the cause of intertidal zonation. The zones are often sharply limited, a fact that is difficult to explain in view of the apparent gradient of physical factors described earlier. Zonation might be caused by varying abilities of different species to tolerate one or more of these physical conditions. Stephenson and Stephenson (1949), who rule out the tidal action per se as producing zonation, believe that zonation is produced by the air-surface interface and the gradients of various factors such as spray above and light penetration below this interface. Elmhirst (1934) suggests the rapid total change in the middle of the intertidal zone compared with the extremities as a cause of zonation.

Doty (1957) suggests that zonation may be caused by regularly occurring differences in heights of successive high tides, which create varying periods of exposure to air (Fig. 8-9). Thus at a high position in the intertidal zone an organism might be covered with water only at alternate high tides, while an organism in a lower position of the intertidal would be covered with each high tide. The organism in the upper part of the intertidal might then be exposed to air for nearly twice the time as the one at the lower position. Moreover, this would mean a rather sharp difference in periods of exposure to air from one level of the intertidal to another. With this scheme, tides themselves would be the factor producing zonation through the secondary effects caused by varying the exposure of organisms to the environmental changes in temperature, desiccation, and other conditions.

ROCKY COAST COMMUNITIES

Physical Features and Adaptations

The rocky coast community is what Marshall (1953) referred to as the balanoid-type biome because of the universal presence of barnacles. The outstanding physical characteristic of such communities is the stability of the substrate, rock.

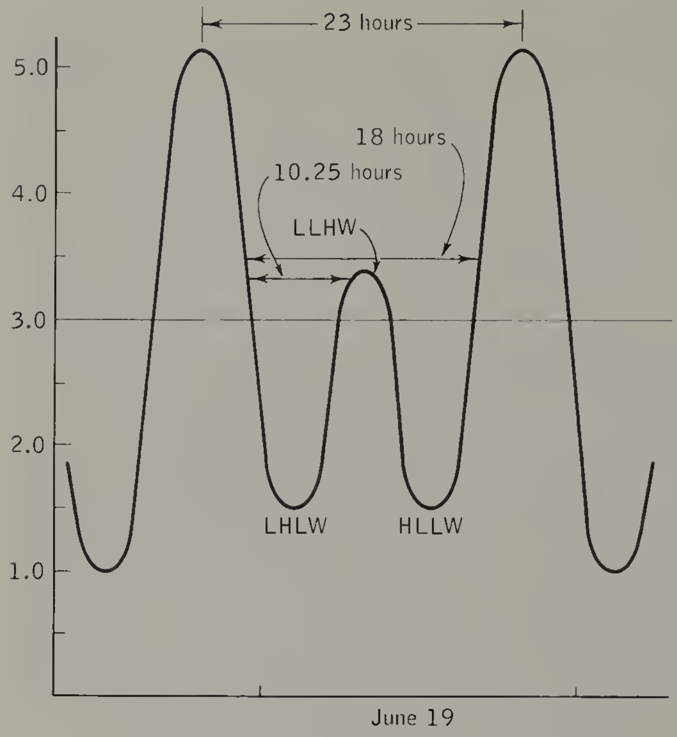


Fig. 8-9 Time of tide levels, San Francisco, California. From Doty, Maxwell. 1947. Rocky intertidal surfaces. In "Treatise on Marine Ecology and Paleontology, Vol. I, Ecology." *Geol. Soc. Am. Mem.* 67. New York. pp. 535–585.

The stability allows organisms which have powerful holdfast mechanisms to remain in place. Thus, although rocky coast communities are often swept by heavy surf and tidal currents, as long as the organism sticks fast to the rock it will not be swept onto the beach or into the open ocean. This adhesion is accomplished in various ways. Algae possess holdfasts. Starfish have many tube feet, while mussels and oysters produce numerous tough threads (byssus) which are glued fast to the rock. Adult barnacles secrete a membranous or calcareous base which tightly adheres to every irregularity of the surface. The sedentary forms especially have heavier skeletons to withstand the pounding surf. A very few species, such as boring clams, attain protection from water movement by boring into the rock, and some hide in crevices or between or under large rocks. Other invertebrates hide among the sedentary organisms, especially algae and mussels.

The attached organisms—algae, barnacles, and mussels—must be able to endure the full brunt of the various consequences of exposure to air when the tide is out. While exposed to air the rock surface may become hot in summer or reach freezing temperatures in winter. Desiccation on bare rocks may be serious, but splashing from waves and capillary action help to alleviate the problem, and fronds of algae, where present, provide moisture as well as protection from extreme temperatures for mobile animals, such as snails, crabs, and isopods.

Zonation of Rocky Beaches

Of all the shore communities, those of rocky coasts exhibit zonation most vividly (Fig. 8-10). Especially where the shoreline rises rapidly and where there are relatively few boulders, one may easily observe this phenomenon. The supralittoral zone is relatively poor in organisms. It represents the beginning of the transition from terrestrial to marine con-

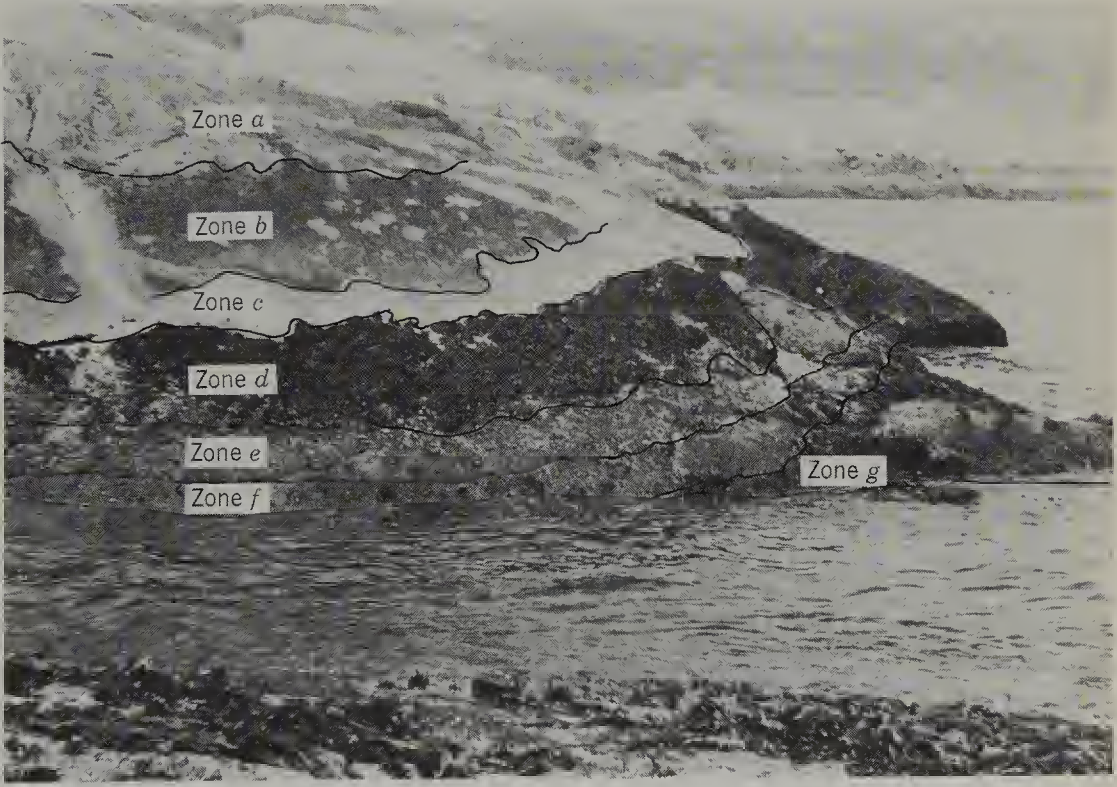


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Fig. 8-10 Rocky shore zonation in Rhode Island. Zone (*a*), Broad bare zone; (*b*) Black zone (blue-green algae, *Calothrix*); (*c*), Red zone (bare in summer; *Bangia*, a red alga); (*d*), Green zone (green alga, *Ulva*); (*e*), White zone (barnacles); (*f*), Black zone (usually mussels, *Mytilus edulis*, here absent); (*g*), Red zone (Irish moss, *Chondrus*).

ditions. In the upper part, the rocks are frequently bare, while the lower region may be covered with blue-green algae or lichens. In warmer climates especially, a large black isopod, *Ligia* sp., is often common. Snails may be present especially at the lower level known as the *splash zone* because wind-blown waves at high tide will spray the area.

At high tide there will be a strand line, composed of algae torn loose from the littoral and sublittoral zones and various other debris. Under the debris, as well as in it, may be found various invertebrates, mostly not permanent residents. In general, the strand line of rocky shores is not as rich in inhabitants as strand lines of other types of beaches.

The littoral zone is sometimes divided into an upper, mid-, and lower zone, although in other classifications the number of zones may be greater or fewer. The upper third of the intertidal is usually occupied by barnacles, and sometimes by snails and limpets. Often green algae, such as *Cladophora* and *Enteromorpha*, may be present. The mid-littoral is frequently dominated by green algae, especially sea lettuce, or by various brown algae such as *Fucus*, and below this by barnacles. In the lower littoral, mussels are often present, followed by red algae, and then near the low-tide line, kelps, which extend into the sublittoral. Red algae penetrate deepest into the sublittoral waters, however. Different species of snails may be found at each of the littoral levels, and the same is true of barnacles.

The Food Web of Rocky Beaches

The rocky shore exposed to surf is in one sense not an easy place for organisms to live. On the other hand, stability of the substrate is so favorable that many organisms are found in this environment. As we shall see, it is especially rich in life compared with sandy beaches, where substrate is exceptionally unstable. Snails may be so thick in the upper intertidal zone that it is difficult to walk without stepping on some. In the barnacle zone, nearly every available inch of space will be occupied, and similarly with the algal, mussel, and other zones. Where one species is so abundant, competition for space and (in the case of animals) for food must be among individuals of the same species, rather than between species. On the other hand, interspecific competition is not altogether lacking, since there are usually several species of invertebrates and algae present in any one zone.

In the rocky shore communities, attached algae provide a good part of the basic food. Phytoplankton are also important as producers of this community. Snails are among the chief grazers on the attached algae, along with limpets. The beach fleas and other amphipods are also important consumers of algae and debris. Barnacles and mussels are filter feeders, ingesting small suspended particles of food. Preying on the barnacles are carnivorous snails, and on the mussels, starfish. Under the thick mat of mussels may be found worms, isopods, amphipods, and brittle stars. Dexter (1947) noted a rhythmical change in the composition of the shore communities with the ebb and flow of the tide. This change is related to food habits: terrestrial animals tend to move down in the intertidal zone at low tide, while subtidal animals move up to feed in the intertidal zone when it is under water.

Tide Pools

Rocky beaches usually have tide pools, and these afford an excellent opportunity to study organisms of surf-lashed rocky shore communities, a task which might otherwise be difficult because of constant wave action (Fig. 8-11*a, b*). Tide pools at various levels of the intertidal zone reflect to a large degree the organisms living at that particular level of the beach when the tide is in. However, some studies have shown that at any one intertidal level the size of the pool may affect the species composition found there.

Artificial Substrates

Man-made structures placed along the coast may serve as a habitat similar to rocky beaches, at least in respect to stability of substrate. Thus concrete jetties or bulkheads provide a rocklike surface or may be constructed with rock fill. On such structures some of the organisms of rocky beaches are usually found, including barnacles, snails, mussels, and algae. Jetties may provide good opportunities for experimentation, since an even surface will eliminate variations which might produce slightly different environmental conditions. Pilings may also present suitable conditions for observing rocky beach zonation, especially when the preservatives have been leached out. On older pilings one may observe the effects of gribbles, isopods which eat the wood. Since they find optimum living conditions at one intertidal level (near mean low tide) and increasingly unsatisfactory conditions away from that point

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(*a*) A tide pool near high-tide line. Rocks provide hiding places for animals. Water flushes in and out (at right) until tide recedes.

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(*b*) Tide pools at mid and low tides. Animals are especially numerous in pools with abundant microscopic algae, as in center left.

in both directions, the result is pilings that appear to have been attacked by beavers! On suitable pilings, however, one may observe many plants and animals, especially barnacles, clams, oysters, tunicates, algae, and various worms, crabs, and other invertebrates. Shipworms (*Teredo* sp.), which are clams highly modified for boring, attack the piling in the subtidal zone. In this zone also hydroids and colonial and simple tunicates may abound. Fish may be found around pilings feeding on this rather rich assortment of organisms, and one type at least, the blenny, makes use of empty oyster shells for a hiding place.

One method of studying organisms that require a stable substrate is to suspend plates of various substances or blocks of wood in the water. Growth rates, reproduction, various physical requirements, and other characteristics of sedentary species such as barnacles and shipworms have been studied in this convenient way. Such organisms, which attach not only to these blocks and panels but also to the sides of ships, are known as "fouling organisms." They must be given economic consideration because of the damage they do to ships and docks and because they slow down ships at sea by increasing friction. In addition, valuable time is lost while ships are drydocked to remove them.

SANDY BEACH COMMUNITIES

Physical Features and Adaptations

The physical feature which is of utmost importance to life on sandy beaches is the unstable nature of the substrate, sand. If there is any surf, the sand will be continually shifted about by water at and below the tide line, and, during storms, even well above normal high-tide line. Wind is an important factor in the supralittoral zone because of its action on the substrate there. Storms often radically alter the topography of a sandy beach, so that it varies from day to day, season to season, and year to year. This extreme substrate instability prevents the attachment of sedentary forms in the intertidal zone and creates conditions in which specialized forms do best in the supralittoral.

There are several other consequences of the instability of sand. Where breakers hit, the water will be boiling with sand particles, creating a potent abrasive action. Tide pools are usually absent, since the shifting sands usually allow drainage, and surface irregularities are soon smoothed out. However, on some hard-packed sand beaches tide pools may occur, and frequently there are marshy areas behind the dunes which may contain brackish water. Where tidal ranges are small, offshore bars often develop, which then alter animal populations of the beach (Hedgpeth, 1957*c*).

Although the instability of sand is unfavorable to most organisms, there are a few redeeming qualities of this substrate which permit some species to inhabit it. For one thing, animals can burrow through it with ease, compared to rock, into which only a few animals can bore. Also, the sand particles allow exchange of gases, especially oxygen. The depth to which oxygen penetrates (the maximum point indicated by the appearance of a black layer) varies from a few inches to over 2 feet according to the surf. Another feature is the size of the sand grains of the beach. Different beaches often have different-sized sand grains, and this will affect various characteristics such as capillarity and therefore the ability of organisms to live there. When the tide is out, an animal need only burrow down a short way and it will find water, since capillary action will raise it above the momentary level of the sea. Wet sand adheres well, and so burrows do not easily collapse. By burrowing, an animal can avoid the extremes of temperatures which must be endured by many of the organisms living on rocky beaches. Salinity changes are also not too great a problem because of the ready availability and circulation of sea water. So it is that most animals that inhabit sandy beaches are burrowers. Interestingly enough, even some of the planktonic algae of this environment migrate up and down, coming to the surface to photosynthesize only when the tide is out (Fauré-Fremiet, 1951).

A few animals in sandy beach communities add still another act to the behavior of these organisms—movement up and down the beach with the tide. One such animal is the mole crab, which stays at the level of the breakers. Certain species of the small coquina clam of warmer waters exhibit this habit too. The exact mechanism of the migrations is still a mystery (Turner and Belding, 1957). Another kind of movement up and down the beach is made by the ghost crab, which stays always above the breakers, digging his burrow above high tide and then making forays down the beach as far as the water in search of food. Thus, for the few species which have the suitable physical adaptations or behavior, the

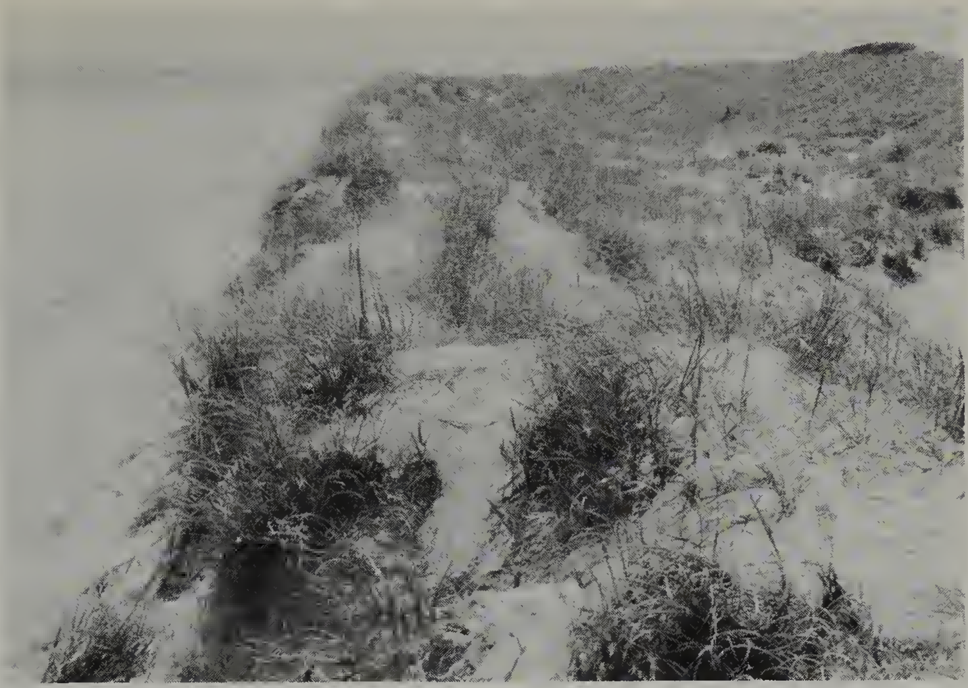

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Fig. 8-12 The supralittoral zone of a sandy beach, Jekyl Island, Georgia. Note the sand dunes to the right and the sparse vegetation near the littoral zone.

sandy beach presents a favorable habitat, and individuals of such species may be numerous.

Zonation of Sandy Beaches

The zonation in the supralittoral zone is usually obvious (Fig. 8-12). The sand of the beaches is blown about by winds, and dunes usually form. Wagner (1964) found that wind is the factor most important in zonation of the dune-strand habitat, because it carries both spray and sand. On the sand dunes, certain characteristic plants are commonly found. The first of these next to high-tide line must be able to colonize sand and tolerate or take advantage of shifting sand. In addition, it must be able to withstand salt spray. Common species in this category are *Ammophila*, sea oats, and other grasses (Fig. 8-13). Higher up on the dunes and farther away from the ocean, one may find other typical plants, including grasses and forbs. On the highest part of the dunes, various species of shrubs and trees usually occur. A characteristic shrub is bayberry (also found in the upper supralittoral of rocky beaches). Many of the shrubs and trees may be species

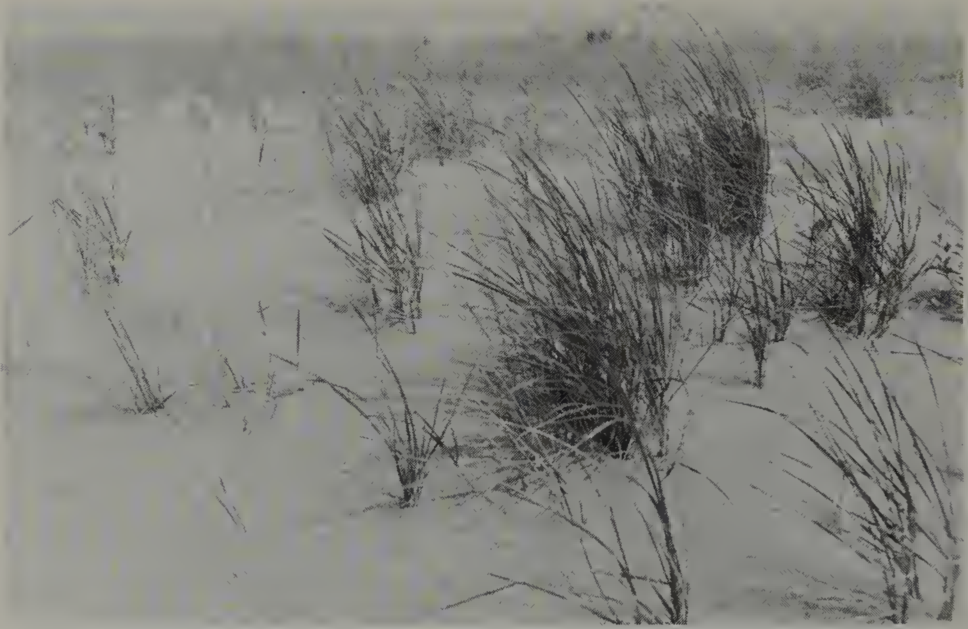

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Fig. 8-13 Beach grass, *Ammophila,* a common invader of the lower supralittoral zone. Rhode Island.

commonly found inland. A phenomenon easily seen on these shrubs is a shearing of the limbs from sand-blasting and salt spray, so that they are taller on the land side than on the sea side (Fig. 8-14). Boyce (1954) showed that one of the contributing factors of the shearing effect was a greater translocation and deposition of the chloride ion toward the seaward side of the plant compared to the leeward side. Thus, only on the seaward side does enough chloride ion accumulate to cause injury, which prunes the plant but does not kill it.

As was mentioned previously, zonation is not easily observed in the littoral zone of sandy beaches. Sedentary forms which are responsible for zonation of rocky beaches cannot live here. The only visible sign of zonation is the strand line (Fig. 8-15). Frequently there will be large amounts of algae washed in at high tide and left stranded. These plants provide food for beach fleas, spiders, and numerous insects, mainly springtails, beetles, and flies, most of which are terrestrial forms. Animals are more abundant in this strand line than on rocky beaches, probably because of the nature of the substrate. The sand provides a reservoir of moisture and is easily penetrated for escaping unfavorable temperatures. Sometimes the rot-

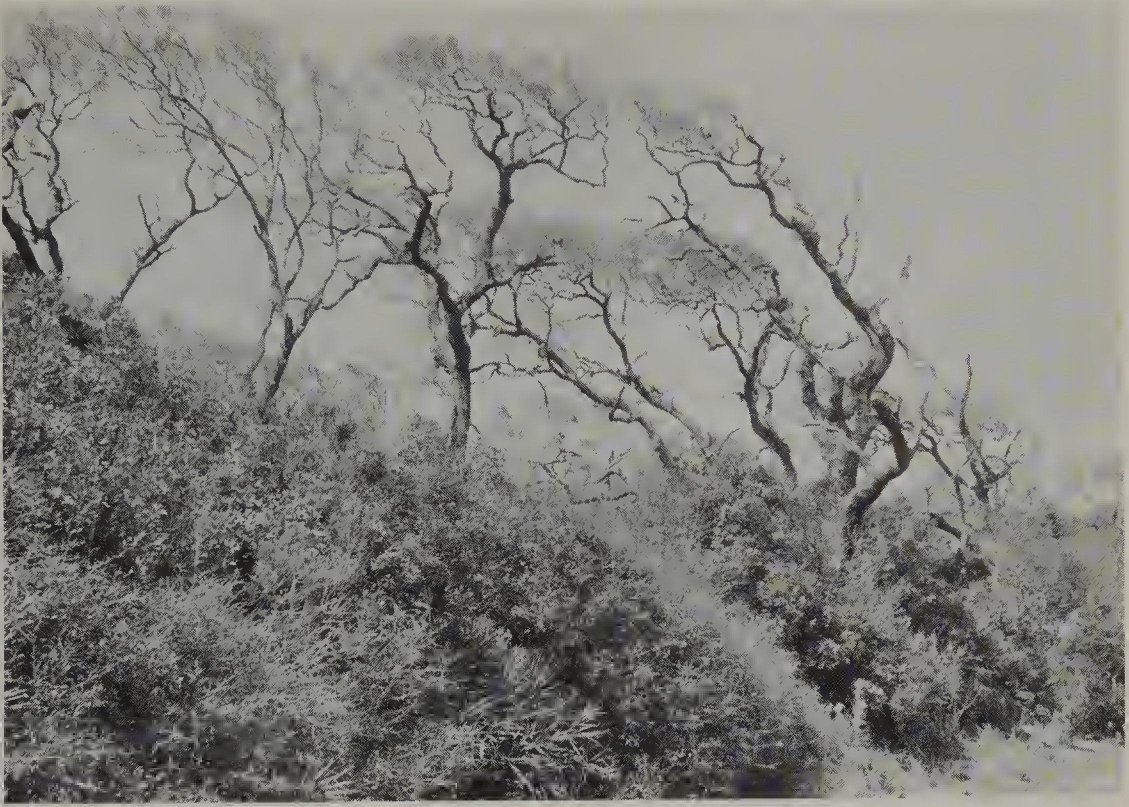

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Fig. 8-14 The effects of salt spray and sand blasting, Jekyl Island, Georgia. Shrubs and trees are trimmed off on the seaward side (to right).

ting vegetation is incorporated into the sand, forming a dark layer.

Although zonation on sandy beaches may not be apparent (other than the strand line), zonation is actually present. Several workers have described zonations based on abundance of different types of animals in the sand. One classification (Dahl, 1953) is based on a zonation of larger crustaceans, another on gastropods (Pearse et al., 1942). There are difficulties with all such proposed classifications, which makes the use of any of them as the universal scheme of zonation for sandy beaches unsatisfactory (Hedgpeth, 1957*c*). However, zonation does occur; it is merely inconspicuous because the organisms of the beach are hidden in the sand.

The Food Web of Sandy Beaches

In the littoral zone, the only basic producers are planktonic algae, especially diatoms. Animals may eat these small plants as well as microscopic animals or organic material in the sand,

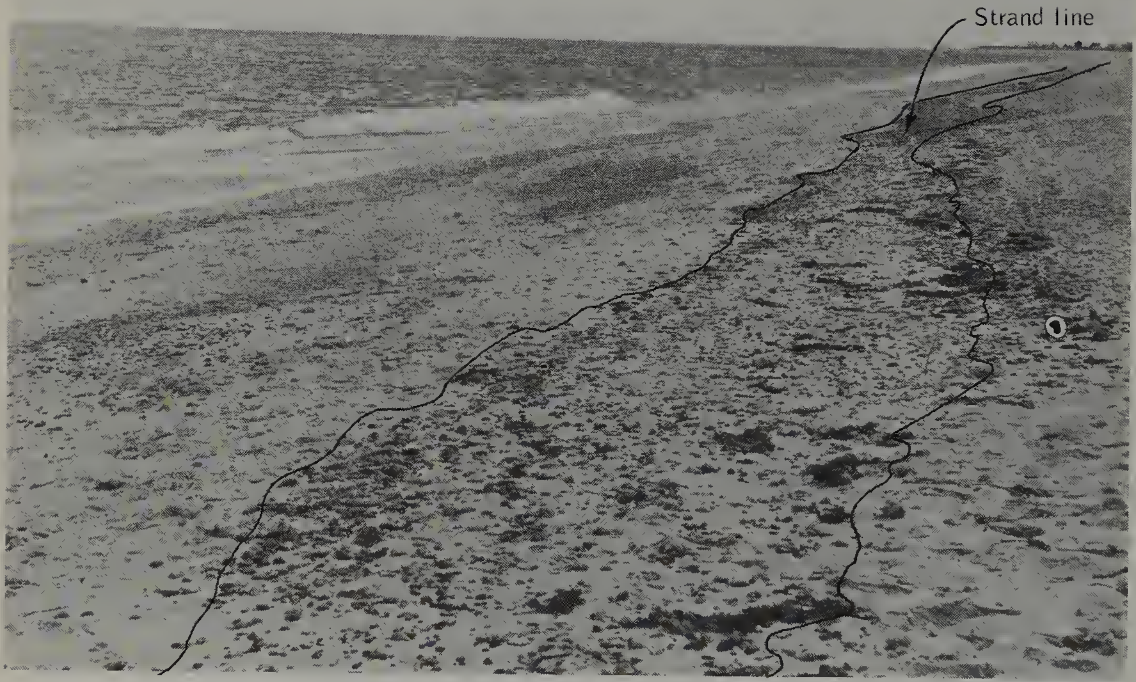

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Fig. 8-15 The littoral zone of a sandy beach in Rhode Island. Surf keeps sand in motion at the water level. Dried algae and other debris form a strand line at high-tide line.

or they may prey on other animals. The sand acts as a trap for organic matter washed in from the ocean, which adds to the available food. Common microscopic invertebrates of the sandy beach include copepods, nematodes, ostracods, and gastropods. Larger animals of the community include *filter feeders* such as clams and mole crabs, and *deposit feeders,* which remove food particles from the sand. Most worms of the sandy beach are of the latter type. Predators include certain nemerteans and snails such as the auger shell and moon snail, which bore holes in other snails and clams. Gulls, terns, and plovers are other predators which frequently visit this kind of community. Sandy beaches exposed to heavy surf may be populated by only a few species of larger animals. Furthermore, a species may be abundant in one location one year and absent the next. If the beach is relatively protected from the surf, the sand may be partly muddy, the beach firmer, and a greater variety and number of animals present.

MUD BEACH COMMUNITIES

Physical Features and Adaptations

Mud beaches or flats are found only in areas protected from surf action. Often they are in estuarian situations, but the discussion here will omit complications caused by fresh-water dilution occurring in such situations. The particle size in mud may vary from silt to a mixture of silt and sand, but an essential feature of this substrate is softness. However, owing to lack of surf action, the substrate remains relatively stable, and so the habitat is more favorable to life than exposed sandy beaches. Among the soil particles organic matter is abundant, but the lack of water movement and the lack of air spaces between the fine particles do not promote rapid exchange of gases. As a result, there is only a surface zone of aerobic decomposition by bacteria. Beneath this, anaerobic conditions prevail which produce the black color and odor of hydrogen sulfide characteristic of this mud.

Mud beaches may be narrow or wide. In any case, topography is usually not perfectly level; so tide pools and

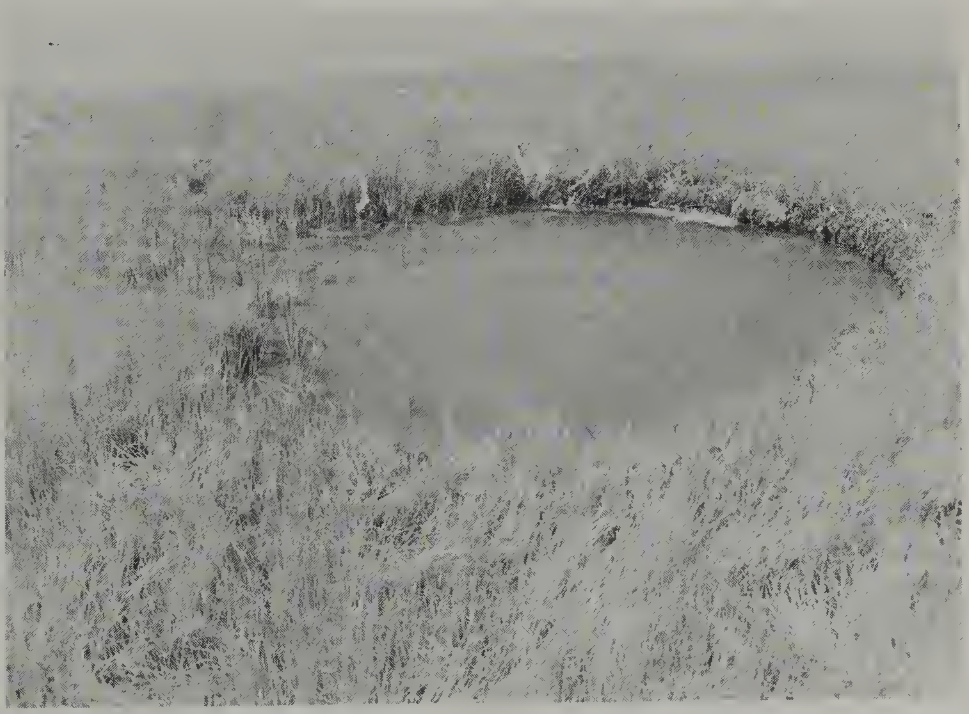

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Fig. 8-16 A tide pool near high-tide line of a muddy beach. Rhode Island.

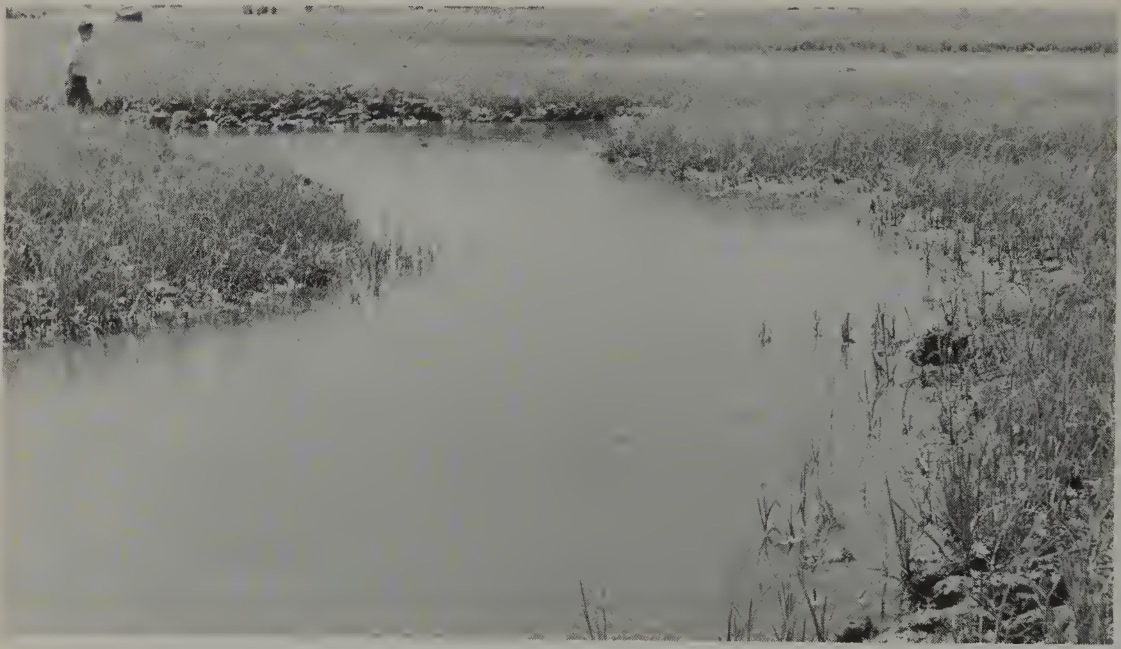

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Fig. 8-17 A tidal stream on a mud beach, with the tide in. Rhode Island.

tidal streams may be found (Figs. 8-16, 8-17). The water in the tide pools will be subject to many of the fluctuations in temperature, pH, salinity, and gas content observed in rocky-shore tide pools.

As we have seen, on rocky beaches the organism which possessed unusual ability to attach or bore was the successful type; on sandy beaches it was the burrower. On mud beaches other adaptations are found. One of the successful types of animals has a tube of some sort which allows most of its body to remain hidden in the mud while it obtains food and oxygen from the surface water, such as clams with long siphons (e.g., geoducks and long-necked clams). Another successful type is one which can dig through the mud horizontally for its food without the necessity of maintaining an open burrow, such as nemertean worms. If an animal does make a burrow, tubes must be constructed to keep a passage open to the surface, since the mud would collapse otherwise. Many worms build tubes, sometimes from sand grains, sometimes from particles of shells and debris. All these types of animals live in the mud. They are therefore called the *infauna*. Another type of animal which does well in this habitat is one which has the ability to remain on the surface of the mud and is therefore part of the *epifauna.* Such animals are able to traverse the mud without sinking in. Examples include the mud snails and sea slugs. Sometimes there are occasional rocks on mud flats, and these may then be covered with algae and sedentary animals such as oysters and barnacles.

The Food Web of Mud Beaches

The food available in this kind of environment is abundant, for mud is loaded with dead organic material. Bacterial populations are high, but hydrogen sulfide in the mud prevents most animals from penetrating deeply. Macroscopic plants are not abundant, except in the supralittoral and sublittoral zones. Zobell and Feltham (1942) found that bacterial populations may be as high as 10 million per cubic centimeter in mud, compared with a few hundred per cubic centimeter in flowing sea water. Such large populations deplete the mud of oxygen and produce the toxic hydrogen sulfide, but they are able to live on organic compounds useless to most animals, such as cellulose. In turn, they are probably an important food item for many infauna animals and so are able to transfer this energy on up the food pyramid.

Detritus feeders are the most abundant animals in the mud, with filter feeders dominating in coarser sediments and deposit feeders in finer sediments. (Detritus includes minute organic matter both in the water and in bottom sediment.) In a study of the benthos of Long Island Sound, Sanders (1956) found the average number of detritus feeders to range from 5,563 to 46,348 per square meter. Predators on these forms include boring snails, nemertean worms, birds (gulls, terns, and various shore birds), and possibly nereid worms. Some workers (Sanders, 1956; Teal, 1962), however, have discovered that at least some species of nereid worms are actually detritus feeders, despite the presence of predaceous-looking jaws.

Zonation of Mud Beaches

The supralittoral zone of a mud beach in temperate climates is usually a marsh, in which there is a conspicuous zonation of plants (Fig. 8-18). Animals reflect the plant zonation, as shown in a study of spiders in maritime marshes (Barnes, 1953). The vegetation next to high-tide line is a marsh grass, and the sod of this grass will sometimes form a miniature cliff at high-tide line (Fig. 8-19). In this sod one

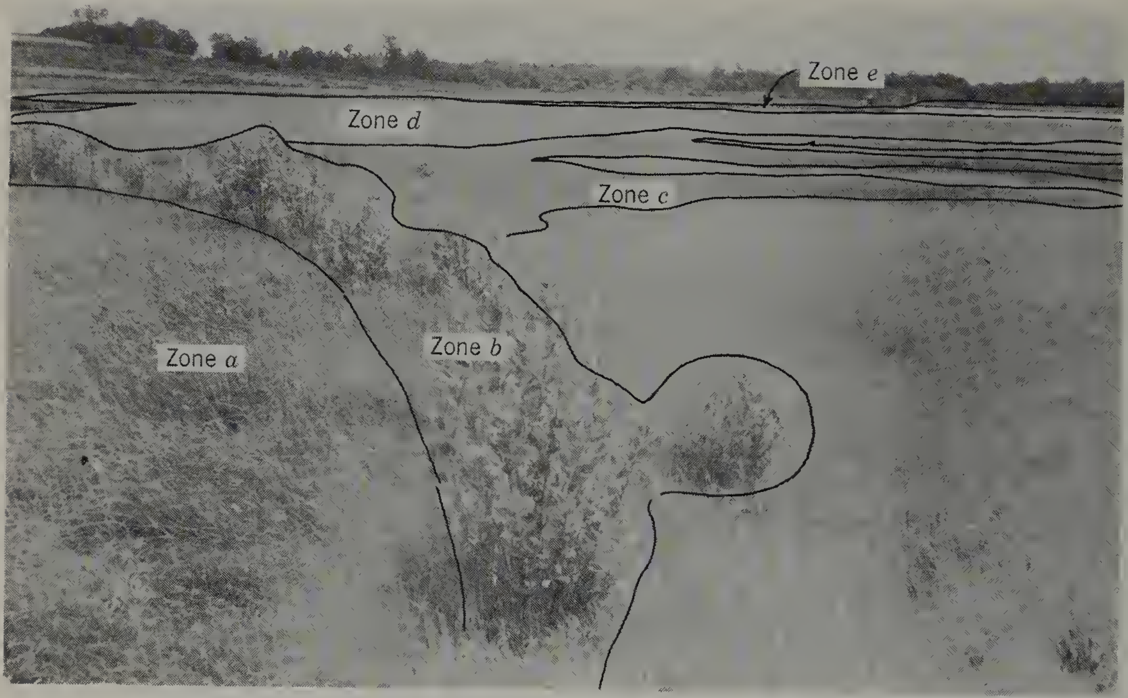

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Fig. 8-18 Zonation in a tidal marsh, Pettaquamscutt River, Rhode Island. Dominants of the zones are: (*a*) Sweet grass, *Hierochloe odorata;* (*b*) High-tide bush, *Iva oraria;* (*c*) the dark area, a rush, *Juncus gerardi;* (*d*) Beyond the rushes, salt meadow cord grass, *Spartina patens,* and salt grass, *Distichlis spicata;* (*e*) next to the water, *Spartina alterniflora.*

may find the burrows of fiddler crabs. Also, near the edge of the cliff, a certain species of clam is often present, with only its posterior end showing above the mud (Fig. 8-20). The marsh grass may be flooded by higher than average tides, and at the limit of the highest tides the strand line will be found with the usual plant, animal, and other debris. Beyond this is often found a zone of finer-bladed grasses, and beyond this a zone of rushes and, eventually, shrubs. Marsh grasses tend to slow water movement and trap sediment. Incomplete decomposition of the marsh grasses due to anaerobic conditions in some cases may lead to the production of peat.

The marsh grasses provide food and cover for numerous animals. Invertebrates typical of this community include leeches, amphipods, shrimp, salt marsh mosquitoes, water beetles, and other aquatic insects. Grasshoppers and snails are common as consumers of the grasses. Top minnows and killifishes are characteristic fishes. Shore birds such as herons, sandpipers, and plovers, and marsh birds like red-

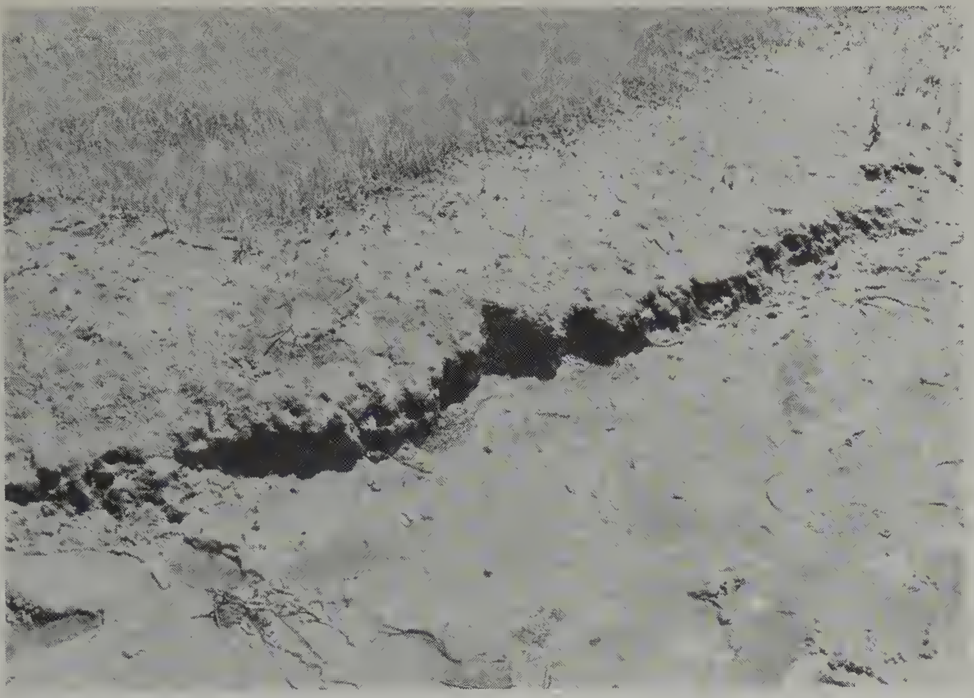

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Fig. 8-19 A small mud cliff, about six inches high, near high-tide line on a mud beach. The plants next to the shore are salt-marsh cord grass, *Spartina alterniflora.*

winged blackbirds, marsh wrens, coots, rails, bitterns, and ducks utilize salt marshes also. In certain localities, voles, muskrats, deer, and raccoon are to be found in this community. Today, many salt marshes are being drained, filled, or in other ways destroyed. This obviously poses a threat for many of the salt-marsh species and may drastically reduce their populations. In some cases extermination may result.

In the tropics, instead of a grassy marsh one finds a mangrove swamp in the supralittoral zone of a mud beach. The mangrove swamp also exhibits a conspicuous zonation (see p. 152). A common animal in this community is the land crab, whose burrows often riddle the soil under the trees above the high-tide mark. One or more species of snails is typically found in the mangroves next to the water.

The littoral zone of the mud beach, like that of the sand beach, is usually devoid of attached organisms and therefore lacks obvious zonation (Fig. 8-21). Near the high-tide line one may come upon hordes of fiddler crabs when the tide is out. In the upper part of the littoral zone there are usually mud snails crawling about. In the central part of the beach

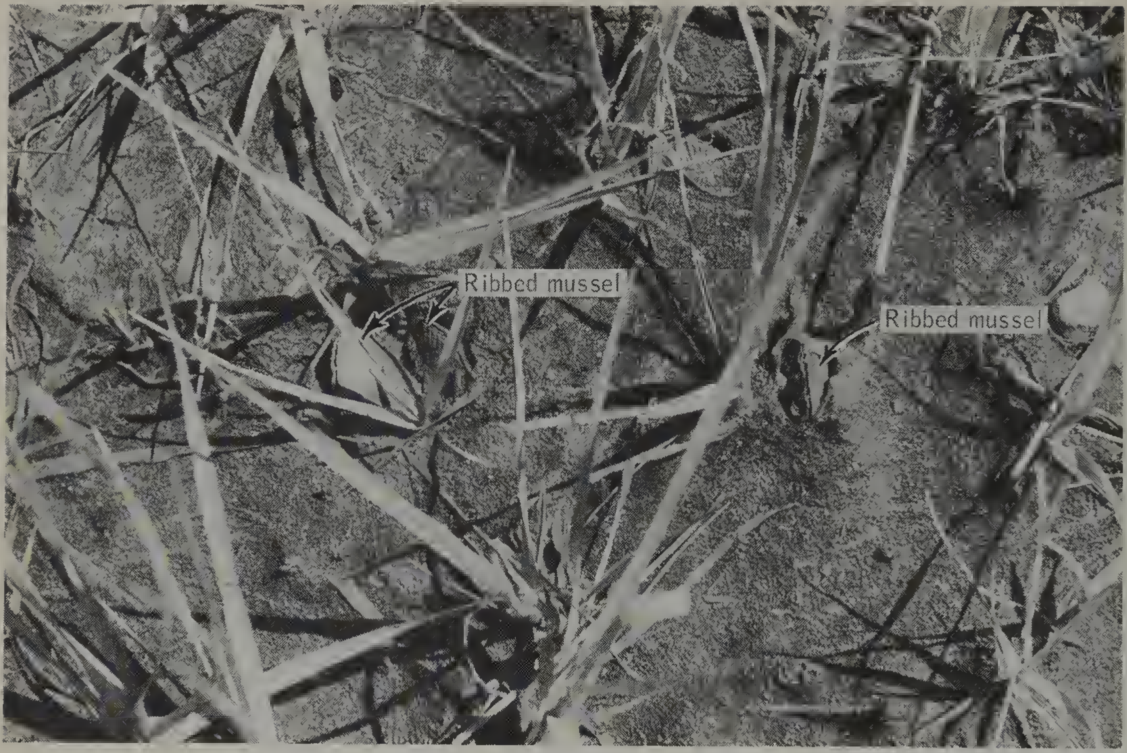

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Fig. 8-20 At the sea edge of the supralittoral zone, among the *Spartina alterniflora,* is the large ribbed mussel, *Modiolus demissus.* Only one end of the mussel protrudes above the mud.

the predaceous basket snails are to be found, and in the mud, clams and worms are abundant. In the lower part of the littoral zone, when the tide covers this region, sea slugs and snails may be seen on the mud, and worms and clams of various species are to be found in the mud. Just below low tide is the zone of eel grass (in temperate climates) and turtle grass, manatee grass, and widgeon grass in tropical waters of the southeast. Among the grass are many species of animals, including shrimp, scallops, sea urchins, sea cucumbers, sea slugs, amphipods, tunicates, and many others. The mud beach is also the home of many fish, which will migrate in when the tide is in. However, the dominant animals of this type of community are worms and clams.

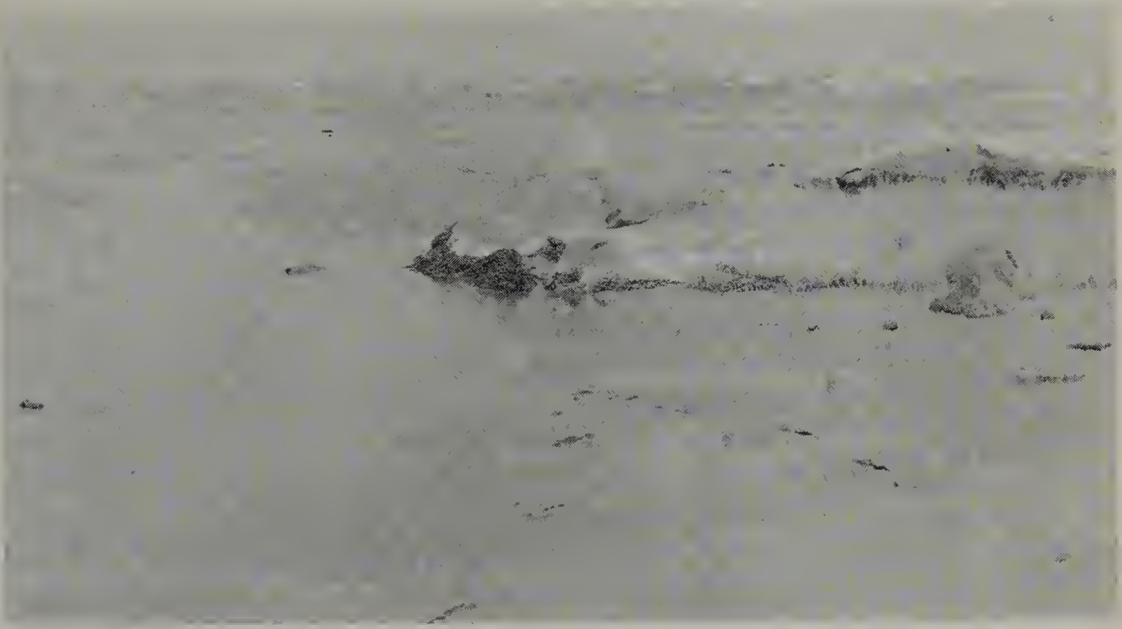

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Fig. 8-21 Littoral zone of a mud beach at low tide. Note numerous tide pools, a tide stream, and attached algae on the rocks.

CORAL REEF COMMUNITIES

Formation and Distribution

As was mentioned earlier, some ecologists feel that coral reefs represent a distinct community type of a rank similar to terrestrial biomes. This distinction is based on their unique character, the completeness of their ecosystem, their complexity, and dynamic "stability." Coral reefs are being simultaneously built and destroyed by organic and inorganic processes, and specific physical and biotic conditions must prevail for such reefs to form and be maintained. Not all corals form reefs. Those which do have rather specific requirements for growth, which tend to restrict coral reefs to certain areas of the oceans.

Among the factors necessary for the occurrence of coral reefs is a water temperature which seldom if ever drops below 70° Fahrenheit. Along the shores of North America, coral reefs are best developed in the Atlantic, where they may be found along the southeastern tip of Florida, the Florida Keys, the islands of the Caribbean, and off the mainland of the southern end of Mexico and Central America. The warm waters of the Gulf Stream also allow the existence of reefs off Bermuda, well above 30 degrees N latitude. On the Pacific coast, the cold California Current and the upwelling of cold bottom waters do not permit development of coral reefs until the southern tip of Mexico, below 20 degrees N latitude (Wells, 1957).

The coral reefs off the Florida coast and the Florida Keys and most of the Caribbean do not protrude above water at low tide, as they often do in the Pacific and Indian Oceans. This may be due to low minimum air temperatures. Wells (1957) notes that these reefs lack algal pavements and indicates this may account for the lack of their extension into the intertidal zone.

Many areas that are warm enough to have coral reefs lack them, however. There must therefore be other limiting factors for their development. One of these is salinity. Reefs do not grow well in diluted sea water, as occurs at the mouths of rivers. Another critical demand is a particular depth, the preference being for relatively shallow water. The depth requirement is undoubtedly a reflection of the fact that within the reef-forming corals are symbiotic algae—zooxanthellae (dinoflagellates), which require light for photosynthesis. In clear water, therefore, the reef corals may extend to greater depths, but the limit is still usually about 180 feet. Coraline algae, which are often found among the corals and which cement the coral together and help to form the reef, also are limited in depth to which they may grow by light penetration.

In addition, there are other biological, physical, and chemical considerations affecting growth of coral reefs. Certain fish tend to erode a coral reef by eating live coral, and some boring invertebrates (clams, sponges, worms) are continually breaking down coral. Storms may destroy parts of reefs by washing away large sections as well as abrading and killing live coral. The growth of corals in shallow waters may sometimes be limited by insufficient oxygen, and this may be involved in growth patterns of reefs. Rapid accumulation of bottom sediment also is unfavorable to coral reef growth. For a description of these and other conditions involved in growth of coral reefs, as well as a discussion of the controversial theories concerning formation of coral atolls, barrier and fringing reefs, see Wells (1957), and Hesse et al. (1951). Studies of coral reefs off the Atlantic coast of North America have been made by Newell et al. (1951), Smith (1948), and Stephenson and Stephenson (1950). For a description of

Pacific coast North American corals, see Durham (1947), and Palmer (1928).

Organisms of Reefs

The limy corals and encrusting algae are major components of the reef and are important because of their action in creating the solid substrate. Encrusting bryozoans may also add to limy growth of a reef. Other sedentary organisms are also conspicuous on reefs. Especially on Florida and West Indian reefs, a leathery or wiry type of coral (gorgonid) is abundant. Examples of these include the sea fan and sea whips.

Coral reef communities are complex. It was noted previously that zooxanthellae (which give corals their color) live within the coral, and that other encrusting algae grow on the coral, cementing the whole mass together. The live coral eats zooplankton, but also derives certain benefits from the zooxanthellae. The corals grow in a porous fashion, creating excellent cover for motile animals. Thus many invertebrates use the coral as hiding and feeding places, and of course these attract other animals to prey on them.

In a recent study performed by scuba diving both day and night off a Florida key, Schroeder and Starck (1964) found that there are actually three groups of animals inhabiting a reef with respect to time and place of feeding. One feeds away from the reef by night and rests there during the day; another forages away from the reef during the day and returns to rest at night; a third group remains on the reef night and day, feeding and resting there.

The Food Web of Coral Reefs

Hiatt and Strasburg (1960) found a complex food web on coral reefs in the Marshall Islands in the Pacific. Algae are the producers in the reef. Some live as symbionts in the coral, some are encrusting, some are boring, and others live in anemones or in dead coral fragments. Algae within the coral are eaten by some fish along with the coral. Echinoderms, mollusks, worms, and crustaceans also feed on the algae. The corals are zooplankton feeders. Other predators on small animals include starfish, mollusks, and worms. Various fish feed near the bottom, eating corals, echinoderms, and sponges. Midway to the surface in the water over the reef another group of carivorous fish live, and near the surface is a third type of fish, also carnivorous. Odum and Odum (1955) concluded that the reef community is a true ecological "climax," as indicated by a dynamic steady state with regard to energy of the ecosystem. They also pointed out that the relationship between algae and coral is comparable in degree of mutualism with that existing between algae and fungi in lichens.

PELAGIC COMMUNITIES

Physical Conditions

A brief description has already been given of the major oceanic currents bordering North America and their general surface temperatures. Under the surface currents there may be other currents, sometimes flowing in an opposite direction. The temperatures of the deeper water are usually much lower than the surface waters. Overturn of water from top to bottom or vice versa occurs only in certain regions of the open ocean. An important factor in this condition is the great depth of the oceans. In addition salinity as well as temperature affects density, and both factors must be considered together when studying movements of ocean water. Surface salinity varies according to local conditions. In general, evaporation increases salinity; precipitation or dilution from rivers decreases it. Currents bring surface water from equatorial regions, where evaporation has increased salinity, to the poles, where it is cooled. Thus, the densest water forms in either the arctic or antarctic regions. This heavy, cold, highly saline surface water descends and spreads out to fill all the ocean basins. Even at the equator, where the surface water may warm to 30° Centigrade, the bottom waters remain cold (Sverdrup et al., 1942). Nonetheless, upwelling occurs at regions other than the arctic and antarctic, primarily along the western coasts of continents (with several exceptions) and near the equator.

The end result of these conditions is that only in limited areas of the oceans is bottom water brought to the surface. Remains of dead organisms and minerals which accumulate on the bottom or are in solution or suspension in bottom waters may remain there for lengthy periods. During this time most of these materials are effectively removed from use in the ecosystem. However, in the occasional places of upwelling, productivity may be unusually high. Ketchum

(1947) found in one such area that 73 per cent of surface phosphorus was made available by vertical mixing, while 25 per cent was supplied by decomposition or organisms at the surface, and 2 per cent disappeared from the surface. Nutrients are, of course, also added to the ocean from estuaries and the littoral regions.

Pressure is a physical condition which may be of significance to organisms living at great depths. Where the great pressures are encountered (as much as 32,000 pounds per square inch in hadal regions) salinity is higher and temperatures are low also. Contrary to popular belief, most organisms do not explode when brought up from great depths, although they often die, probably because of higher temperatures encountered near the surface. Pressures are equalized in organisms living at any one depth, but some animals migrate considerable distances up and down within short periods of time. Bruun (1957), in surveying the literature on the effects of pressure on organisms, concluded that organisms living in hadal depths must have special physiological adaptations allowing them to withstand pressures that produce paralysis in other animals.

Of great significance to life in the sea is light penetration. The exact depth to which light penetrates varies with the factors which affect the amount of light reaching the surface and the absorbent nature of the water. Thus altitude of the sun, cloudiness, contamination of the air by dust, etc., as well as turbidity of the water, organisms in the water, and surface turbulence, will all affect light penetration. The compensation depth may be as deep as 135 feet, but this is shallow compared with the total depth of the water. The greatest part of the ocean waters is therefore below this zone of effective photosynthesis (*euphotic zone*). Not all light, of course, is extinguished at the compensation depth and some continues to penetrate to 600 feet or more (*photic zone*). Below the photic zone (which includes the euphotic) is the region of darkness (*aphotic zone*).

Pelagic Food Chains

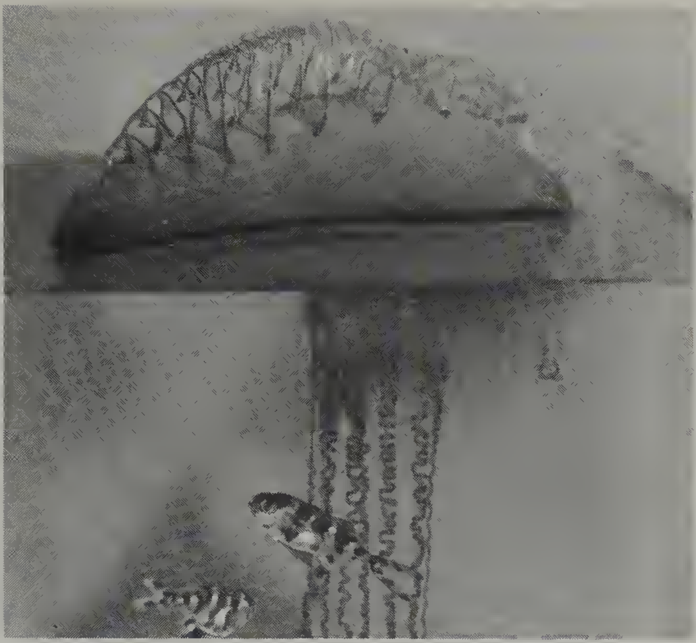
In the open sea, the depth to the bottom is obviously too great for the survival of attached benthic plants, although some diatoms do live at great depths. The only pelagic organisms which can fix the sun's energy are the microscopic algae. The greater part of these plants are diatoms, and to a lesser extent, dinoflagellates. They can, of course, effectively photosynthesize only in the shallow euphotic zone. Upon their organic production, all the animals of the open ocean, from the surface to the bottom, are dependent. The food chain from these primary producers to the ultimate carnivore is long, passing through several levels of consumers.

In many areas of the oceans, productivity is restricted by lack of sufficient nutrients. The nutrients required by diatoms include phosphates, nitrates, iron, manganese, silicates, and trace elements. Greatest productivity is attained when these substances are present as part of organic compounds (Nigrelli, 1963). These organic metabolites are produced originally by phytoplankton. When they die, bacterial action breaks down their protoplasm, releasing the organic compounds. Bacteria, plants, and animals may also secrete some of the substances used by the phytoplankton, including organic acids, enzymes, vitamins, and other compounds. Often the compounds are incorporated into bottom muds. The amount of dissolved organic matter in the sea is actually greater than the particulate matter at any one time (Sverdrup et al., 1942). As important as nutrients are to productivity, they are not the only factors involved. Thus Riley (1952) found that the major factors affecting phytoplankton productivity include light, temperature, sinking of the algae below the euphotic zone, phosphate depletion, rate of respiration, and grazing by zooplankton.

Zooplankton are the primary feeders on phytoplankton, although certain fish such as mullets, anchovy, herrings, and mackerel also feed directly on the microscopic algae as well as on the zooplankton. Some whales also feed on such small fare. Copepods, especially *Calanus* sp., are among the common zooplankters. Much of the zooplankton will die without being eaten and fall toward the bottom. Bacterial decomposition will then reduce their protoplasm to organic compounds.

Squid and fish such as tuna, barracuda, salmon, and shark are the larger predators of the epipelagic zone, but smaller ones also occur. Thus there are the floating Portuguese man-of-war and violet snail, and submerged but frequently abundant, sea walnuts, comb jellies, jellyfishes, and siphonophores (Fig. 8-22).

Below, in the mesopelagic region, there is no light. Especially abundant are euphausid shrimp and sergestid prawns which feed on plankton. Most of the other animals of this



Charles E. Lane

Fig. 8-22 Portuguese man-of-war and its commensal, *Nomeus gronovii.* The fish avoid contact with the stinging nematocysts, even though they find shelter among the tentacles.

region are predators, including squids and various fishes (Fig. 8-23). There is a tendency for the fishes to be red or black. Fishes with large eyes and luminescent organs, such as lantern fishes and hatchet fishes, are common. Some of the animals from this region migrate to the surface at night.

In the mesopelagic zone at tropical and subtropical latitudes, when the temperature drops to about 10° Centigrade, a change in the fauna occurs. Bruun (1957) suggested the change occurs because animals living at greater depths cannot tolerate the warmer surface temperatures. However, by using sonar recordings in a study of the depths at which animals are found, Dietz (1962) came to the conclusion that it is not temperature, but light which is responsible for this change of fauna. He points out that the depth at which the 10° isotherm occurs varies with latitude, occurring closer to the surface near the poles, but the sonar recordings show no similar change in depth of the populations with latitude.

In the bathypelagic zone are various kinds of animals, including other species of prawns, squid, and fish. In general there is little tendency of animals of this region to migrate

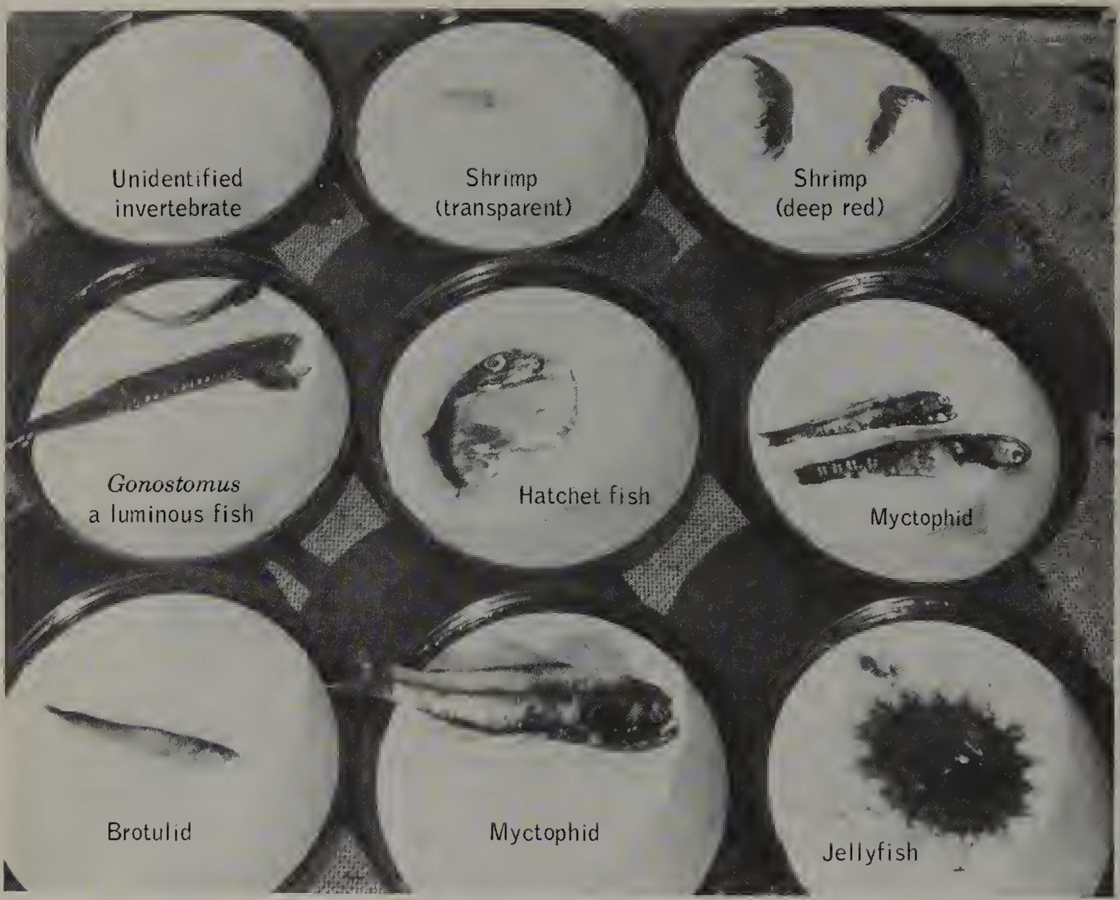


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Fig. 8-23 Animals from a deep plankton net haul near the bottom (about 2,100 feet) in the Gulf of Mexico, south of the Dry Tortugas. The specimens are in bottle caps 3¾ inches in diameter. Top row: an unidentified invertebrate and two species of shrimp. Middle row, from left: *Gonostomus*, a luminescent fish; hatchet fish; and a myctophid, also luminescent. Bottom row, from left: a brotulid, a myctophid, and a jelly fish.

upwards. Nearly all animals of this zone are red or black, and many exhibit bioluminescence. A striking type of fish of this region are the deep-sea anglers, so called because of a luminescent organ which they dangle in front of their mouths as a fishing lure. Food is not abundant in this region as it is near the surface, and consequently organisms are fewer.

At approximately the point where the bathypelagic zone ends, the temperature is near 4° Centigrade, although the depth at which this temperature is reached may vary 1,000 meters. Animals of the abyssopelagic region are still fewer than in the bathypelagic. Representatives include different species of deep-sea anglers, crustaceans, worms, and radiolarians. The abyssopelagic continues to about 6,000 meters. Beyond this point, in the hadopelagic, little is known of the fauna. In his dive in the Mariana Trench, Piccard (1960) saw small jellyfish at 32,500 feet and shrimp and a flatfish on the bottom (35,800 feet, about 11,000 meters).

BENTHIC COMMUNITIES

The benthos of the littoral and inner sublittoral zones have been mentioned previously. Some of the earliest quantitative studies of marine life were done on shallow ocean bottoms by C. G. Peterson and more recently by Thorson (1957). In the outer sublittoral, and continuing into the hadal zone, all food energy must ultimately come from other areas of the sea, since photosynthetic plants do not grow there. In the outer sublittoral zones animal populations are large. Turnover of nutrients is good because of the shallowness of the water. Also, when pelagic organisms die, many of them reach the bottom before decaying or being eaten. Organic matter and dead organisms are thus abundant on the bottoms in this region; so benthic populations are high.

On deeper bottoms, organic matter becomes less abundant as productivity in upper waters is also less. Even more important, there is a greater distance for dead organisms to sink, allowing more time for bacterial decomposition before reaching the bottom. Thus, with increasing depth, benthic populations tend to decline in numbers. Bacterial populations at least may be high, and there is lack of agreement as to whether benthic animals may feed largely on bacteria instead of detritus in the mud (Bruun, 1957).

Bottom organisms in deeper water are often more numerous than organisms in the pelagic zone just above them (Fig. 8-25). This reflects the food source in or on the bottom. Since the original food is either parts of dead organisms or organic compounds, the first organisms in the food pyramid are small—for example, bacteria, worms, crustaceans, and sponges. On these smaller organisms, larger animals will feed, so that a distinct benthic food chain is established. This is one of the reasons why some students of the benthos such as Thorsen feel that benthic aggregations constitute distinct communities. The organisms of the benthos are also taxonomically different from those inhabiting the pelagic zones above. Also, from region to region at similar depths, bottom

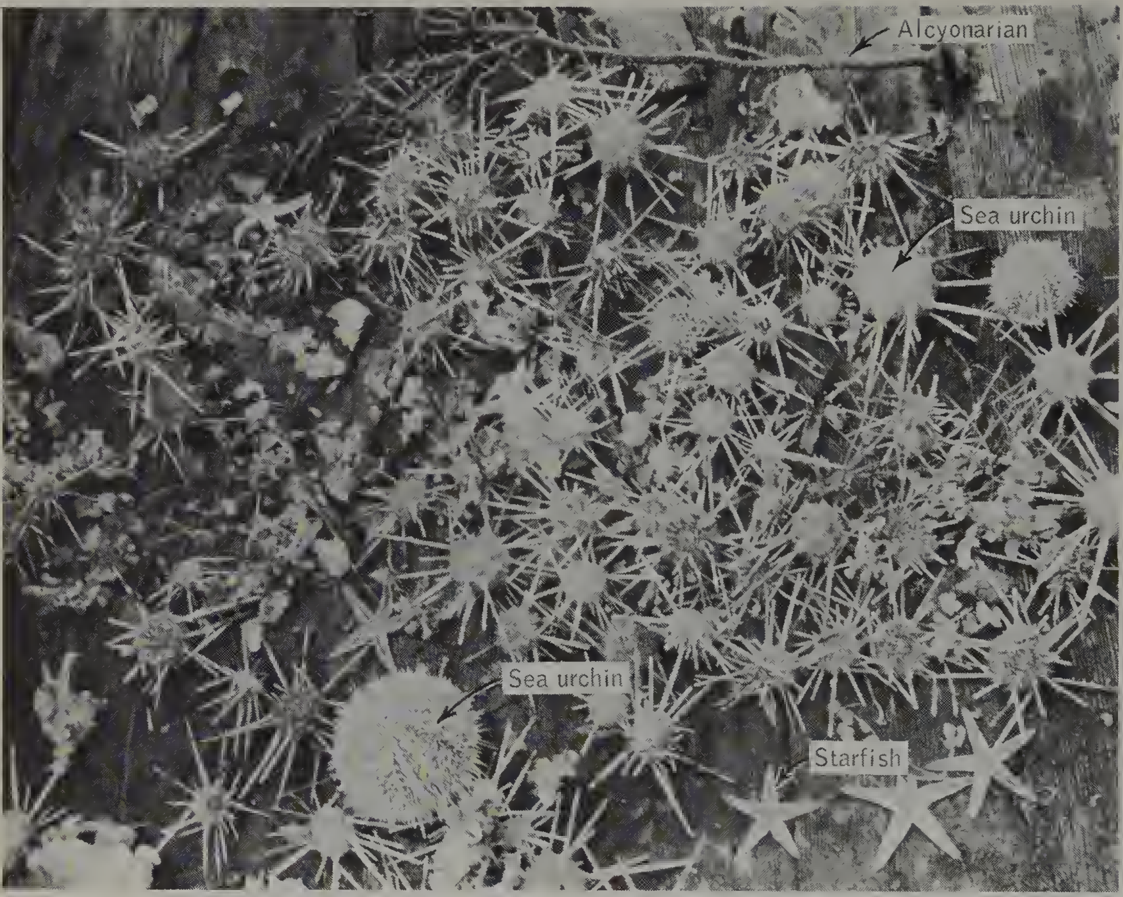

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Fig. 8-24 Benthic animals from the Florida Keys, taken with a bottom trawl from 300 meters. Sea urchins were dominant in this haul, while starfish were also common. The branched animal on top is an alcyonarian, the first specimen of this species known to science. Other animals, caught at the same time but not shown here, included brittle stars, bryozoans, sea anemones, hermit crabs, spider crabs, sea spiders, and fish.

faunas are remarkably alike. Other workers, such as Odum (1959), point out, however, that the benthic food source is in the pelagic or coastal regions and that the benthos and pelagic organisms are members of the same ecosystem. Also, they feel that the pelagic and benthic organisms at any one depth belong to the same community.

Typical abyssal forms include many species of echinoderms, especially filter-feeding holothurians, echinoids, and crinoids, and predatory ophiuroids and asteroids. Other animals of this zone include worms, ascidians, mollusks, shrimp, sponges, coelenterates, and fish. Although sufficient collecting has not yet been done, it appears as though most abyssal species are widespread over the ocean floors, with few distribution barriers (Bruun, 1957).

Hadal fauna is even less perfectly known than the abyssal. Animals of types similar to the abyssal are found (for example, holothurians are again common). Some workers expect that with more research it will be shown, as is already known in a few cases, that related animals living in isolated trenches will belong to separate species (Bruun, 1957).

The depths of the oceans still offer more biological surprises than any other region on earth. New species are being found continually. Often, species are known from only one or a few specimens or from only one locality. Many species have strange anatomical features as adaptations to their life in the deeps. Unraveling the anatomy, physiology, taxonomy, ecology, and distribution of these forms presents a fascinating challenge to future biologists.

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chapter 9

Natural populations

In the early development of biology, great emphasis was placed on thorough study of the individual organism as an example, or "type," of the species. We still use this approach in such fields as comparative anatomy, but in many fields of modern biology variations are as important as similarities. Variations are the raw material of evolution, so to speak, and they are also the key to many important aspects of plant and animal life.

We cannot, of course, study variation without studying individuals, but we must study many rather than one. Thus has developed the modern concern with the population—the individuals of a given species which exist in a given area at any one time. It is usually not possible to examine an entire population, but we can examine a significant fraction of a population and from it draw statistical inferences with regard to the entire population.

In an earlier chapter we pointed out that modern tax-

In all things there is a sort of law of cycles.

Tacitus

onomists work with series of specimens, and they attempt to analyze a significant sample of the species, often with complicated statistical procedures. The same is true of the wildlife biologist, the behaviorist, the plant ecologist, and many other field biologists. As Leopold (1933) has pointed out, "some properties are not discernible in the individual, but only in the mass." Such characteristics as intraspecific tolerance, sexual habits, maximum and optimum density, and other numerical and distributional data are discernible only by a study of the population.

POPULATION PROBLEMS

In the study of populations, our first concern is with *numbers*. How many individuals of a given species are there in the area under scrutiny? How do their numbers vary from time to time? Even more fundamental, why does the population vary, and what factors control these variations? What percentage of a game population is taken by hunters each year? What portion of a timber crop should be removed by lumbermen? Questions of this sort are of basic importance from both the scientific and economic points of view, and unless we have some idea of the answers to these questions, we are seriously deficient in our understanding of the organisms we are studying.

Important as it is, learning the approximate number of a population and other related facts is not enough. We must next consider the *distribution* of the population. How is the population distributed throughout the range of the species? How large an area is occupied by one individual or one family group? What are the climatic, ecological, and physical boundaries of the range of a population? How dense is the population in the most favorable areas?

Another basic property of a population is its *composition* with regard to age and, in bisexual species, sex. Wildlife managers are especially concerned with fairly precise knowledge of this factor. Ecologists, whether interested in plants or animals, need to know the relative abundance of the various age classes in a given habitat. The fluctuations and changes in these factors over many years in plant communities, and from year to year in animal populations, are matters of great importance.

A problem of animal ecologists which is not shared by students of the plant kingdom is *behavior*. This cuts across the other above-mentioned fields to some degree in that distribution and composition of populations may be related to behavior. But behavior also includes social habits, sexual relationships, population movements, and innumerable other characteristics which are best studied at the population level.

An adequate understanding of population dynamics requires information from all these aspects. Much of the basic work remains to be done, and population studies of both plants and animals take a prominent place in journals devoted to ecological studies. We must therefore consider in some detail the population characteristics which we have mentioned and the techniques by which the information we have about them has been acquired.

Population Counting

The first step in understanding population phenomena is to count organisms with reasonable accuracy. At first glance, this might seem relatively simple, but in fact it is fraught with difficulties (cf. Dice, 1941).

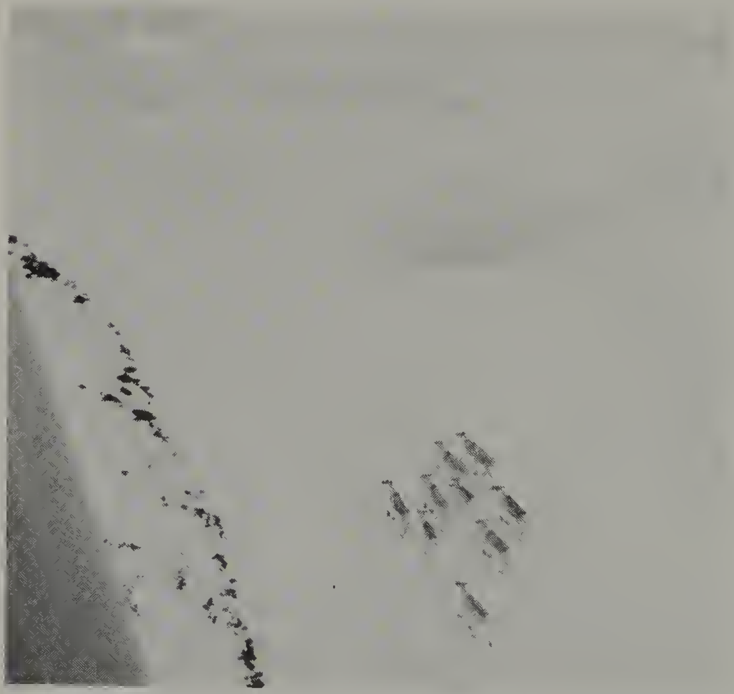
First of all, natural populations do not remain constant in numbers for any appreciable period of time. Animals are being born, plants are starting from seeds, and death is removing members of the population. Some plant populations, especially long-lived species, may remain constant long enough for the biologist to complete his study, but even these species show fluctuations in population from year to year. With small plants and animals, the length of the life cycle may be so short that the size of the population can change drastically in a few days.

Secondly, no natural population is uniformly distributed over its entire range. An accurate appraisal of the population, therefore, must include samples from areas of both high and low population. Each sample must be adequate, and an adequate number of samples must be taken. This brings us to the question of what constitutes an adequate sample. Unfortunately, there is no single answer, but it is safe to say that the sample should be as large as is practical. An ichthyologist working with a large net may be able to collect several hundred fishes per sample and thus use a much larger sample than a mammalogist who has to collect his specimens with live traps, which take only one specimen at a time. The student of insects may be able to examine more individuals than the student of elephants. A sample which might do for a student of redwood trees could well be quite inadequate for a student of grasses. Generally speaking, the reliability of the data will be directly related to the size of the sample, so that a large sample is desirable. An idea of the required sample size may most easily be obtained by reading some recent papers which concern problems similar to the one under study.

In addition to adequacy of size, a sample of a population must be unbiased, or random. Any form of selectivity on the part of the worker must be avoided. A census of songbirds based on singing males may be biased if the number of females or nonsinging males is not accurately known. A census taken in an area of high population is biased if applied to other areas where the population is lower. A census based on live trapping may be biased if males have a larger range or show greater activity than females. The greater the student's knowledge of the species, the less likely that the sample will be biased, if he uses care to prevent bias from occurring.

Despite all these difficulties, the techniques of counting populations have been worked out to an amazingly refined level. The most obvious method, when it is feasible, is direct count. Even though it may not be possible to count all those in the area under consideration, the number in a portion of the area may be counted, and the total number calculated by extrapolation. The direct-count method is used in estimating waterfowl populations, in counting big-game animals, and in computing populations of any animals which are abroad during the day and can be readily seen. It is, of course, the method of choice when counting plants.

Numerous adaptations of the direct-count method have been devised. Airplane counts made either directly or from aerial photographs are useful in making both waterfowl and big-game surveys (Fig. 9-1). This method may not always give an absolute count of the population, but it will indicate



A. T. Bergerud

Fig. 9-1 A herd of caribou photographed from an airplane for census purposes.

relative numbers from year to year. Such information may be sufficient to satisfy the needs of those interested in management or control. Song counts of breeding bird populations, brood and covey counts of game birds, airplane counts of beaver houses, and many similar methods have also been used successfully.

In a majority of cases, however, animals cannot be counted accurately by simple observation. Even when direct counts are feasible, it may be desirable to check the accuracy of the count by a different method. For this purpose, a variety of indirect methods have been developed. The oldest and probably the most widely used is the Lincoln-Peterson index, developed independently for waterfowl by Lincoln and for fishes by Peterson. This method depends upon introducing into a given population a number of marked individuals, such as banded birds, tagged fishes, or toe-clipped mammals. At a later date, a sample of the population is removed and counted. Theoretically, the relationship between marked and unmarked individuals in the sample should be the same as in the population as a whole. Thus $P:M = p:m$, when P equals the total population, M equals the total number of marked individuals in the population, p equals the total of the second sample, and m equals the number of marked individuals in that sample.

As an example, suppose that a fishery biologist takes 250 bass from a lake, marks them with numbered tags, and releases them. A week later, when they have had ample time to become distributed throughout the population, he nets another sample, this time securing 320 bass. Of these 320 fishes, 80 are marked. The formula can now be set up: $P:250 = 320:80$. The total population thus equals 80,000/80, or 1,000 individuals.

This method, as Adams (1951) and others have pointed out, makes several assumptions which may not always be warranted. If the marks are not permanent, or if they put the marked animal at a disadvantage and thus lead to higher mortality in the marked group, or if marked animals are either more or less difficult to catch than unmarked animals, or if the population changes greatly between the first and second samplings, the results may be very misleading. To reduce the error inherent in these possibilities, many biologists have turned to statistical analysis. There are several ways to check the probability that the results are statistically significant, but one of the most often used is determination of the standard error of the mean. With adequate samples, the probability is that the actual population will be within plus or minus two standard errors of the mean of the estimated population; the actual probability is 95 per cent or 19:1, and this is considered significant.

A more detailed discussion of statistical methods may be found in numerous papers and books. Davis (1960) and Quick (1960) have discussed analysis of animal populations, while Phillips (1959), Greig-Smith (1957), and Cain and De Oliveira Castro (1959) have discussed vegetation analysis. A brief discussion of statistical analysis will be found on p. 455, while additional references will be found at the end of this chapter and at the end of Chap. 13 (p. 424).

Population Fluctuations

One aspect of populations which has engaged the attention of biologists for many years is the manner in which fluctuations occur. Leopold (1933) divided animal populations into three types on the basis of these fluctuations (Fig. 9-2). Some animals maintain a relatively constant population level, with only minor fluctuations occurring randomly over a long period. This may be called the *nonfluctuating* type, if we keep in mind that this term is relative. A second type has rather regular ups and downs in numbers, with great variation

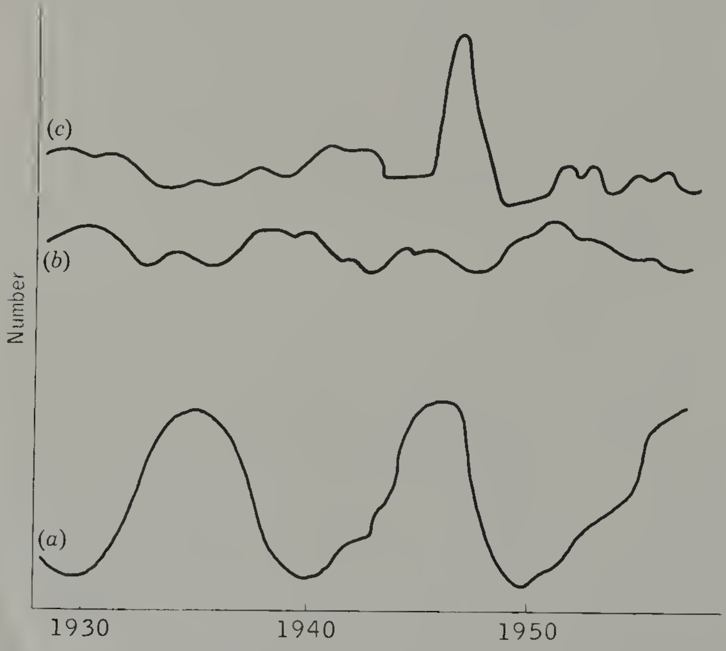


Fig. 9-2 Three common types of population curves: (*a*) cyclic, (*b*) nonfluctuating, (*c*) irruptive. (After Leopold, 1933.)

between high and low points. This we may call the *cyclic* type. The third type is that which has periodic increases and declines in numbers, often reaching a very high density but without any cyclic regularity; that is, with high population densities not occurring at any fixed time interval. This may be called the *irruptive* type of population.

In the United States, for example, the bobwhite quail tends to maintain a relatively stable population in a given area. Unless the conditions of the environment are changed drastically, the population will be relatively nonfluctuating. The ruffed grouse, the snowshoe hare, and the field mouse (Fig. 9-3), however, have regular and fairly predictable cycles, ranging from extreme profusion to an almost complete extirpation. An example of irruptive population growth is that of the house mouse in Kern County, California, in 1926. Hall (1927) estimated that the population in a limited area of highly favorable habitat reached more than 80,000 mice per acre (the equivalent of about 200 mice in a 9- by 12-foot room). Fortunately for human beings, such irruptions are relatively uncommon and do not appear to occur in all animal species.

Since populations show such distinctly different patterns

Ralph S. Palmer

Fig. 9-3 The field mouse, *Microtus pennsylvanicus*, has a population cycle of about three years. At the high point of the cycle they may reach fantastic levels in numbers.

of variation, one can hardly expect to find a single cause which will explain all such fluctuations. Early students of the problem tried to explain these phenomena in terms of such causes as disease, food supply, changes in habitat, and even sunspots and moon phases. After a number of detailed studies had failed to bring agreement on any single cause, a number of ecologists, including Palmgren (1949) and Cole (1951), suggested that so many variables are involved that the resultant fluctuations are quite random. A summary of these and other theories will be found in Hewitt (1954).

Many biologists, however, are not willing to accept the theory of random causation, and the study of population fluctuations has continued unabated. Currently two major schools of thought have developed among those who feel that there is some basic cause of fluctuations and that this cause should be discoverable. One group insists that each population has some intrinsic control mechanism which acts to prevent populations from increasing to extreme highs or falling to extreme lows and that the changes reflect the relative success of this mechanism. Chitty (1960) has postulated such a mechanism, a tendency of a population to deteriorate in quality as it increases in numbers. Subsequent decreases which appear to be caused by disease or other external factors might thus be ascribed to this intrinsic weakness rather than to external factors per se.

Wynne-Edwards (1959) agrees that an intrinsic density-dependent factor exists but presents evidence to show that this factor is social behavior rather than population quality. When populations increase, he argues, territorial demands and other social responses result in a halt to the increase before the population is decimated by such density-independent factors as the food supply.

Still another proponent of intrinsic mechanisms is Christian (1950 and in numerous more recent papers). His theory is based upon the medical theory of Selye (1946) that certain diseases or malfunctions are caused by failure of the organism to adapt to stress. Increasing populations cause new or increased stresses of intraspecific strife, constant contact, greater competition for food and space, and so forth. When these stresses become sufficiently intense, says Christian, an increase in adreno-pituitary activity follows, with eventual breakdown of these endocrine functions and resultant death of the animal. Christian's position has been supported by the experimental data of Frank (1957), Curry-Lindahl (1963), and others.

The stress theory, however, has been subjected to searching criticism by many equally competent field biologists. One of the most detailed analyses has been made by Negus et al. (1961). They suggest that social contact does not necessarily increase as the population increases; that adrenal weight is affected by factors other than stress; that reproductive failure as a result of increasing density has seldom been recorded in natural populations and in any case might be caused by other factors than social stress; and that the role of nutrition in population control is neglected or at least relegated to a subordinate position, whereas their studies and that of others would indicate it is of primary importance.

Most of the work which has been done on population theory among the vertebrates has been concerned with those species which demonstrate a cyclic population fluctuation, and the theories we have discussed apply primarily to such populations. Indeed, the work on which these theories are based has been done on a small number of birds and mammals. We have stressed these studies because they represent some of the major contributions of the field biologist to population theory. Much work has been done on a number of invertebrate populations in the laboratory by Park (1932 and later papers) on the flour beetle, *Tribolium confusum,* and by Slobodkin (1959) and others on *Daphnia.* A great body of work on insects has been included in the book by Andrewartha and Birch (1954). The general conclusion which one might reach after reviewing these studies is that fluctuations are not caused by a single environmental factor. Indeed, there are dozens or even hundreds of factors which affect the population at any given time and in any given species. Probably both extrinsic and intrinsic factors are operative at all times, although time may show that there is indeed one primary cause of cyclic fluctuations at least. A controlled study of a population in nature is virtually impossible, and two reasons for the disagreement which is currently evident are the divergence in interpretation of the available field data and the varying degrees of acceptance of the basic premises which a field worker must make. On the other hand, we are not certain to what extent we can accept the findings of laboratory experiments as explaining natural phenomena in the field. Certain facts, however, are reasonably clear:

1. Each population fluctuates around a central point which may be thought of as optimum density.
2. Optimum density varies with the environment and thus is not constant for all populations of a species.
3. Each environment has a "carrying capacity" for each animal species, but this, too, may vary with time.
4. When a population exceeds this carrying capacity, it will eventually decrease, usually going well below the optimum density.
5. No general explanation of these decreases can be given; indeed, there may be no general cause which is applicable in all cases.

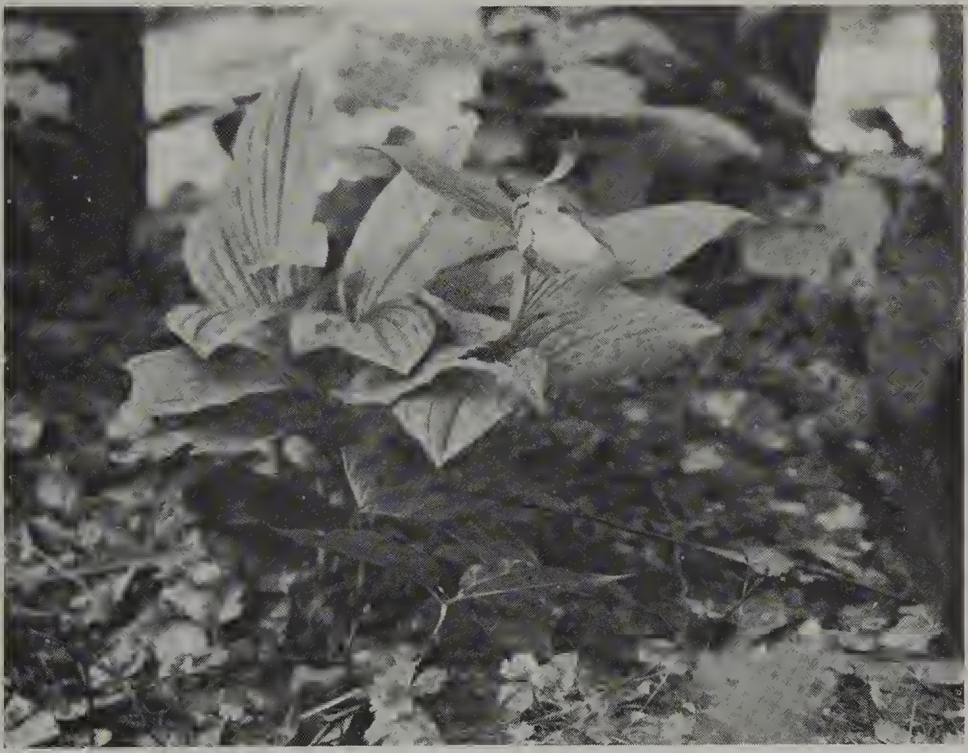
The application of mathematical procedures to population studies, and the development of stochastic population models, along with improved techniques for field study, may herald important advances in our understanding of population fluctuations. We may be sure, at any rate, that this important aspect of field biology will not be neglected and that the bewildering array of theories will continue to be subjected to testing and criticism as long as the current uncertainties remain.

DISTRIBUTION OF POPULATION MEMBERS

The distribution of the members in a population, and of the population as a whole, is fairly easy to learn for plants and for large diurnal animals. Much of the work of early biologists in any area was concerned with demarcating geographical ranges, and to some extent this job is a continuous one, for geographical distribution changes as time goes on. During the past fifty years, for example, there has been a gradual northward extension of many birds and mammals, especially the cardinal and the opossum, and quite possibly a similar change has occurred in many less easily observed plants and animals.

But distribution involves more than simply knowing the geographical range of a species. We also want detailed knowledge of ecological distribution: the preferred habitat for each species and the ecological factors which govern its occurrence. We need more knowledge of the reasons for the limited distribution of some forms and the much wider distribution of similar forms which, to us, show no evident superiority. Some species have become extinct within man's memory because their habitat changed or was destroyed, and they were not able to adapt to the new conditions. Certain species survive in limited areas, as Jeffrey's pine in California and Kirtland's warbler in Michigan. Many of our native orchids (Fig. 9-4) occur in a limited range of ecological situations, as do many other plants and animals. Some of these species have evidently traveled up an evolutionary blind alley to the point of no return. It is important to find out what the limits of tolerance are for each species in regard to habitat. This information is of special value for species which are of economic importance and may be subject to management.

Even after we have learned the ecological range of a given species, we have not learned all we need to know about distribution. The distribution of the members of a population in relation to each other is a matter of the greatest importance. Reforestation with tree species which cannot grow close together would hardly be practical; stocking of game species which would then promptly scatter to the four winds would



Allen H. Benton

Fig. 9-4 The yellow lady's slipper, *Cypripedium pubescens*, an uncommon orchid with rather precise habitat requirements. Allegany State Park, New York.

be expensive and useless. We must understand these phenomena from the economic viewpoint, but they are equally important from the purely biological viewpoint, since they play an important part in the lives of the organisms concerned.

In the case of animals, their distribution in relation to each other is closely related to their social behavior. Howard (1920) first pointed out that birds have definite territories, and we now know that the concept of *territorialism* can be extended to include many other forms of animal life. *Territory* may be defined as that part of the animal's range which is defended by its occupant against members of the same species. This is part of the animal's *home range*, an area traveled by the individual while carrying on its daily activities (Fig. 9-5). In a breeding colony of grackles, which nest colonially, the territory might include only a small portion of the tree in which the nest is built, while the home range would include feeding grounds up to several hundred yards away, a watering place elsewhere, and all the area between these points. In some cases the territory is defended because of its importance during the breeding season, such as the nesting territory of birds, and territorial activity is not usually seen at other sea-

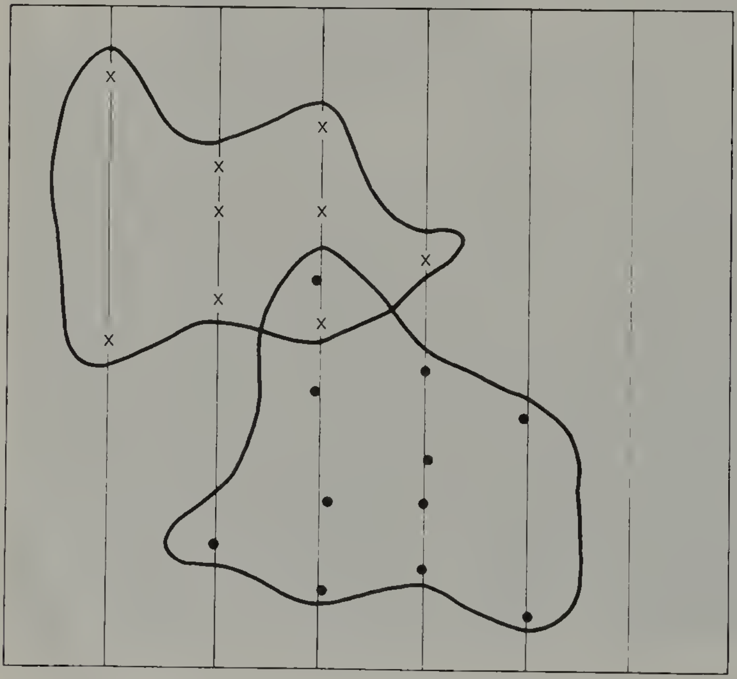


Fig. 9-5 Home range of two mammals as estimated from repeated recaptures in live traps set in a grid.

sons. Sometimes a feeding territory is also defended against other members of the same species.

Territorialism is fairly easy to observe in birds and larger mammals, and we know with a high degree of accuracy the extent of both territory and home range for many species. Nocturnal or subterranean species, however, present special problems, as do species too small to be readily observed. Home range and territory vary, in most species, among different individuals, and vary to some degree with habitat type; availability of food, water, and cover; season; sex, age, and condition of the individual; and other factors. It follows that the determination of these areas must be a somewhat complicated procedure. Because much of the basic work has been done with small mammals, they will serve to illustrate some of the problems and some of the approaches which have been fruitful in determining territory and home range.

Live trapping has been one of the most profitable techniques in the study of home ranges. In this technique, traps are set in a regular pattern, or grid, perhaps six feet apart in each direction. When an animal is captured, it is marked and released. If captured again, it can be recognized and its movements can be plotted with successive recaptures to form a clear and accurate picture of the home range (Fig. 9-5). This technique, of course, requires repeated captures and continued study over long periods. Since the lifetime of most small mammals is quite short, and since repeated recapture may affect the animal adversely or result in changes in behavior, there are some reservations as to results based on this method. Hayne (1949), Stickel (1954), Calhoun and Casby (1958), and others have resorted to statistical analysis in order to overcome the shortcomings of grid trapping. The area of the home range is most frequently delineated by drawing a line halfway between the last trap in which the animal was captured and the next trap in which it might have been captured had it gone that far. This is known as the boundary-strip method, and it allows for the fact that the animals presumably range, on the average, halfway to the nearest trap beyond the one in which they were captured.

The home-range diagram which results from such studies is generally circular or oval. Stumpf and Mohr (1962), however, reported that home ranges in certain mice which they had studied were more linear than circular. They suggested that this is the rule rather than the exception, and that the degree of linearity may vary with the suitability of the range.

A few species have been studied by a different method which appears to produce more consistent results. A radioactive mineral is attached in some manner to an individual animal, which can then be traced with a Geiger counter. Godfrey (1954) found it possible to record a single individual up to 50 times, a result seldom achieved by grid trapping. She used cobalt-60 attached to the vole by a specially constructed leg band, which protected the animal from radioactivity. Her data indicated that home range of animals recorded less than 20 times was not accurately determined. Since many of the determinations made by grid trapping have been based on fewer records than this, it seems likely that many of our conclusions have been in error.

Another modern development in the study of animal movements has been the use of colored dyes. New (1958) pioneered the technique, which consists of capturing one or more small mammals and feeding them with dyed bait. An alternative would be to place dyed bait in an area and note the colored droppings, but in this case one cannot ascertain the number of animals involved. Droppings are collected by placing a number of small squares of board or hardboard, about four inches square, in a grid pattern over the area to be studied. Many small mammals appear to favor these sites for depositing feces, so that their movement during the period of retention of the dye can be determined with some accuracy. Haresign (1960) found that meadow mice, *Microtus*, will retain the dye for 72 hours if a small quantity of Kaopectate is added to the bait or food. In this period enough droppings are usually deposited to permit fairly accurate determination of home range. It must be assumed, of course, that the dye and any additives do not affect the activity of the animal during the period of the study, if the results are to be accepted.

Equally modern is the development of tiny transistorized radio transmitters which can be attached to or even placed within an animal. Such techniques have been used successfully on such diverse animals as woodchucks and deer (Cochran and Lord, 1963), although they are obviously not suitable for use with smaller animals at the present time.

Territorialism is even more difficult to determine in small or secretive animals than is home range. Observation of intraspecific strife is difficult and, even when observed, may not be easily ascribed to the true cause. Fighting may occur over mates, food, or for other reasons, and territorial strife may not be recognized as such. Captive animals may be more readily observed, but it is not certain that captivity does not alter behavior patterns. In this area of study, therefore, a great deal of basic work remains to be done.

Plant Distribution

Each species of plants, also, has a pattern of distribution in relation to others of its kind. Competition for the necessities of life may be just as intense as, though less obvious than, in animals. The pattern of distribution may also be affected by the manner of seed distribution. Wind-blown seeds, such as those of pines, cattails, and grasses of certain kinds, will be distributed in dense colonies in any suitable habitat downwind from existing individuals. Seeds of various sticktights are carried about by animals, attached to their fur. The seeds are dropped at some distance from the parent plant in an entirely random manner. Seeds of jewelweed and witch hazel are thrown a short distance from the parent plant by special adaptations within the seed pod. Thus the area immediately surrounding the plant is soon saturated with seeds which will germinate the following year.

Intraspecific tolerance, however, may also play an important part in the distribution of plants in relation to each other. Some species of trees will not grow in the dense shade of their own kind, and such trees must of necessity be scattered. Others will grow only under the protective canopy of adult trees of their own species, and we often find pure dense stands of such species. A study of plant succession (Chap. 6) indicates that this phenomenon is largely based on changing conditions which make it possible for new species to take over an area. Such tolerance or intolerance is, of course, not active, as it is in animals. It may be based on physiological characteristics of the seedling plant. But it results in a varied pattern of distribution, just as in animal species.

The space utilized by each individual and the manner in which that space relates to spaces occupied by other individuals are important and basic properties of each species. Refinements of existing techniques and the development of new techniques can be expected to increase our knowledge of these phenomena and to improve the accuracy of the information available.

AGE AND SEX COMPOSITION OF POPULATIONS

Enough has been said to indicate that it is not always easy to discover even the basic facts about a population. The factors which govern density, distribution, and fluctuations in populations are simply too varied to be readily determinable. Yet the biologist who wishes to know any species thoroughly must know far more than numbers and distribution. Of primary concern, particularly to the men charged with management of wildlife populations, is the composition of the population with regard to age and sex. In those species which are hunted or trapped, it is necessary to establish seasons, bag limits, and other regulations which will assure a sustained yield of the species for the future. The total take by human agencies, added to natural mortality, must not exceed the annual increase, or the whole population is in danger.

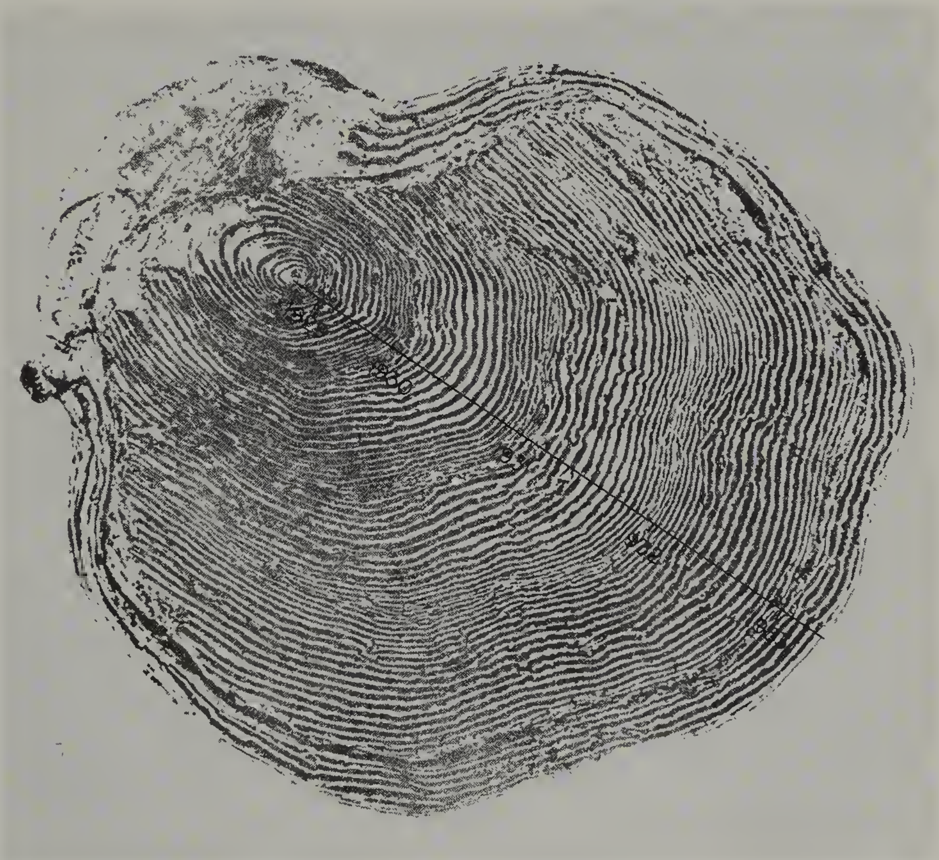
Age Composition

In a population which is living within its biological means, in other words, which is maintaining its numbers at a more or less steady level, a definite kind of age composition will appear. Just what this may be will depend to some extent upon the life pattern of the species. Life tables for most species are not available (Deevey, 1947; Quick, 1960), but it is evident that in any species there should be enough surviving young at the end of each breeding season to replace the adults which died during that season. In short-lived species, the annual turnover may be 100 per cent. This is true of a good many insects, but of very few if any birds and mammals.

If a population survey shows a preponderance of old animals and an unusually small number of young animals, it may indicate that natural mortality is not sufficient to remove the older animals. Possibly the population is too large, and inadequate nutrition is inhibiting reproduction. If there are many young and very few older individuals, it may indicate excessive mortality of adults, such as might occur when only adult animals are legal game. It is obvious that these facts are of both theoretical and practical significance.

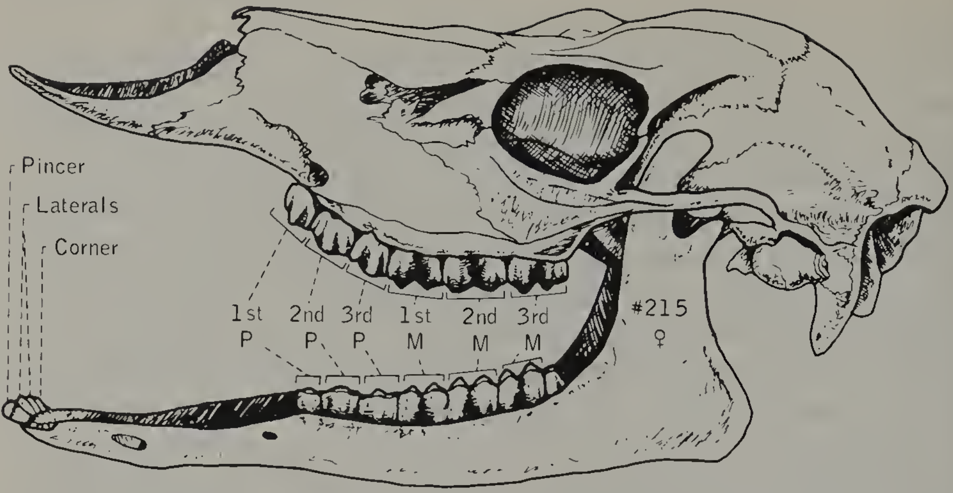
To determine the age composition of a population, one must first learn to recognize the various age classes. For a few groups, techniques are available by which biologists can do this. In mammals, tooth eruption and tooth wear are most often used (Fig. 9-6). In birds, the color and condition of the plumage may help, and in some groups the bursa of Fabricius, a blind sac within the cloaca, may be measured as a criterion of age. In fishes, the scales show rings (Fig. 9-7) which permit determination of age in much the same manner as do the rings of trees. By checking the large numbers of specimens which are taken each year by hunters and fishermen, large samples of the population may be examined, and a statistically valid picture of the population may be obtained. Such knowledge is necessary if intelligent management procedures are to be instituted (Fig. 9-8).

For many, indeed most species of animals, even the techniques of age determination are not known. Taber (1960) has reviewed the techniques used with birds and mammals,



N.Y. State Conservation Dept.

Fig. 9-6 Age of a fish can be determined with a high degree of accuracy by the microscopic study of its scales. The width of the bands varies with the season.



N.Y. State Conservation Dept.

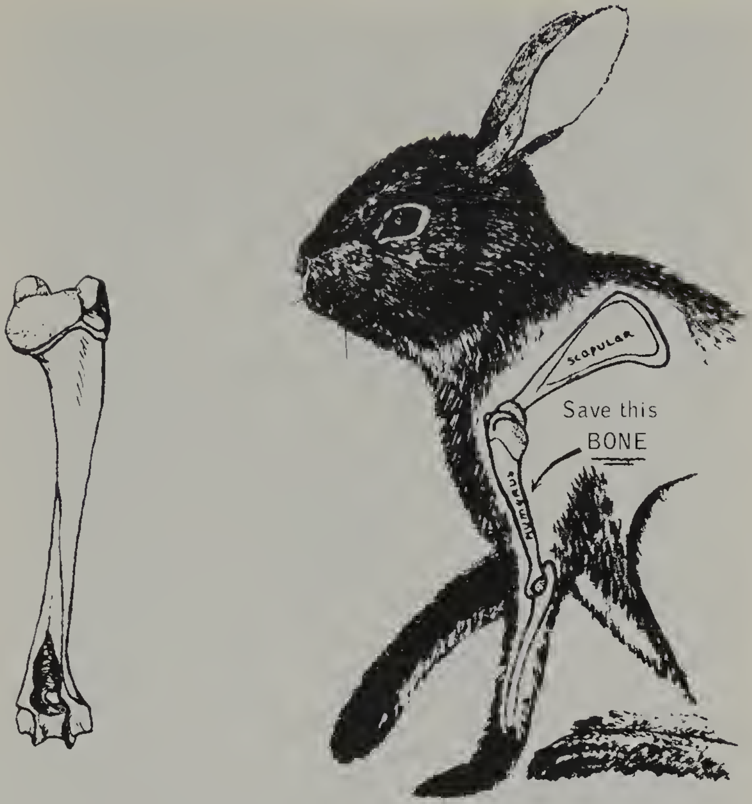
Fig. 9-7 Tooth development and wear are age criteria used in studies of deer populations.

but for many groups little or no information is available. For those groups which live long enough for such data to be of significance, biologists will have to continue to build on the foundation of knowledge currently at hand.

Sex Composition

In most species, the sex ratio at birth is assumed to be about one male to one female. By adulthood, the ratio may change in favor of the females in the species with significant sexual differences in habits, color, or some other characteristic. A preponderance of females would do no harm in polygamous species, and, indeed, is probably quite normal. This is the basis of laws protecting the females of many game species, from ring-necked pheasants to white-tailed deer.

This very protection, however, may lead to serious imbalance of the sex ratio. The white-tailed deer is an example of this situation. Only antlered bucks may be taken in most states, and those with large antlers are most desired by hunters. Thus the females and the young of the year are protected from hunter damage, and in most of the range the other possible predators are relatively unimportant. After many years of such regulations, the population may show a very high ratio of females and an equally unbalanced age ratio. In such cases, it may be necessary to declare an open season on antlerless deer in order to bring both the sex ratio and the age ratio into more normal proportions.



N.Y. State Conservation Dept.

Fig. 9-8 New York State hunters collect the humerus from the cottontail rabbit to provide age data for game managers.

Just what "normal proportions" are, however, is not quite so simple to determine. Full utilization of the reproductive capacity of any species demands that all females capable of reproduction must be impregnated. The number of males necessary to perform this essential task is variable, and in some cases (e.g., Canada geese), the ratio must be 1:1. Only by a careful study of the breeding biology of each species can we ascertain what percentage of the males are biologically essential and what percentage can be treated as surplus. For many economically important species, these facts are known. For many others, our data are imperfect, and further study is necessary.

POPULATION BEHAVIOR

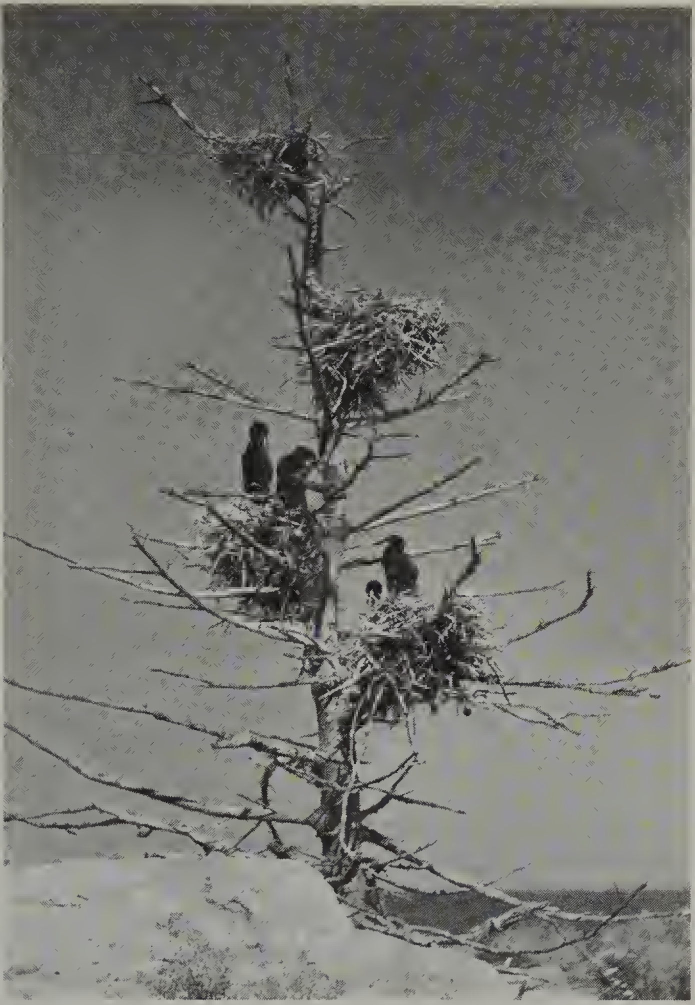
The behavior of individual animals is considered in some detail in Chap. 10. We are concerned here, however, with the behavioral characteristics which cannot be seen in a single individual but which are nonetheless characteristic of the species. These phenomena are concerned with intraspecific relationships that occur when animals are together. For convenience, we may divide the occasions on which animals are together into two categories: animal aggregations, which are temporary, and animal societies, which are permanent as far as the individual goes.

Animal Aggregations

Temporary aggregations may be formed for a variety of reasons: for migration, as in many species of birds; for protection against predators and other environmental hazards, as in musk oxen; for feeding, as in wintering herds of deer; for breeding, as at the mating grounds of prairie chickens; for nesting, as in the double-crested cormorants (Fig. 9-9). Animals may band together in family groups which may include several to many families. Such aggregations are usually based on a biological requirement that seems to cause an instinctive desire for association with other individuals of the species. Often animal aggregations are intimately concerned with the survival of the individual and of the species.

In game species, a knowledge of the occurrence and functions of aggregations is essential to sound management. An open season at the time of such aggregations may be dangerous to the survival of the species. The extinction of the passenger pigeon was probably brought about mainly by overexploitation while they were in breeding colonies and migratory aggregations. Spring shooting at the mating grounds of the prairie chickens and open seasons on the close-flying flocks of migrating shore birds once threatened these species with extinction. Biologists who determine hunting regulations must give careful attention to these aspects of population behavior.

Some animal aggregations may result in better protection from the environment because of increased alertness or the strength of numbers. The feeding bands of crows, with at least one member always on watch for enemies, are less vulnerable to attack than any one individual. On the other hand, concentrations of prey species usually attract predators, which may leave to return again and again, or may remain nearby. Wolves hang on the fringes of migrating caribou herds, alert to secure the weak or careless. Lions follows the great herds of African grazing animals as they move to new feeding areas,



Ralph S. Palmer

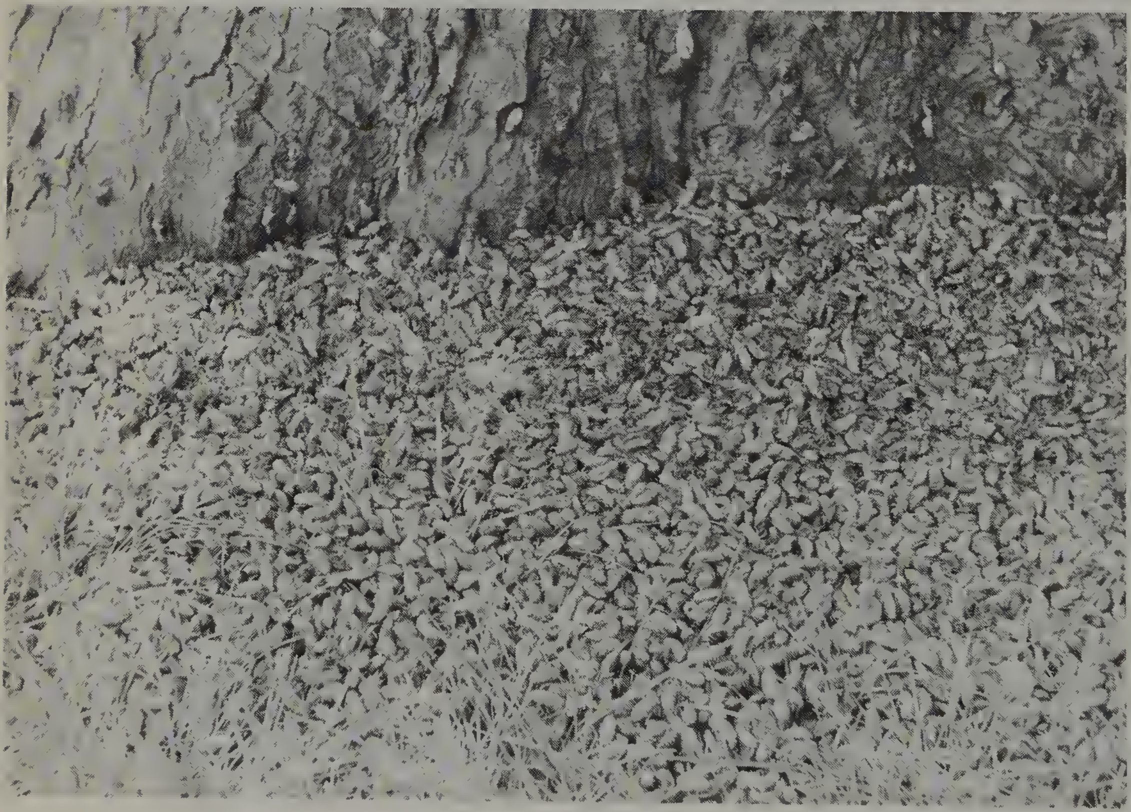
Fig. 9-9 A breeding aggregation. Double-crested cormorants nest in colonies, sometimes doing considerable damage to the vegetation.

cutting off and devouring an occasional individual. Hawks and owls haunt the roosting areas of birds and bats, and the sharp-shinned hawk in particular has learned that the numerous winter feeding trays are good hunting places. Natural predation of this sort usually succeeds only in maintaining the prey population at the normal carrying capacity of the environment. Human beings, with their more efficient weapons of destruction, however, may decimate these groups of animals so severely as to cause their eventual extinction.

Although temporary aggregations are best known from their occurrence in large or obvious species, they occur in essentially all groups of animals. The student of the natural history of the species will find such gatherings important to his understanding of the species and will also find it easier to collect, examine, or study large numbers of individuals when they are gathered together (Fig. 9-10). The student of population dynamics will be able to take, mark, and study large numbers of individuals. It is no accident that the largest number of banded birds are taken during periods when aggregations are present, thus adding much to our knowledge of bird biology. The student of behavior will find many interesting facets of behavior elucidated when groups are together, which would be unexplainable or might not even occur when individuals are alone.

Animal Societies

Many animals live in association with other members of their species in a more or less closely knit society. These societies are characterized by permanence, lasting throughout the



William E. Werner, Jr.

Fig. 9-10 A mass of nymphal shells and emerging adults of the periodical cicada. These aggregations occur briefly every 17 years when the insects emerge to mate.

lives of the individuals which make up the group. Indeed, the societies are usually essential to the life of the individual and thus to the existence of the species. Such groups may be very complex, based on a rigid system of order and on the precise, instinctive actions of the individuals in the colony.

Because human society is such an important aspect of our own existence. we have a marked interest in subhuman societies, and this interest has shown itself among biologists and non-biologists alike for many centuries. The Biblical writer who suggested that lazy men might well consider the ways of the ant had evidently noted that insect's bustling activity. Other philosophers such as Maeterlinck have been fascinated by the seemingly intelligent operation of a hive of bees.

Animal societies show tremendous variation in organization, and it is tempting to think of them in terms of our own experience. Most animal societies, however, are much more rigid than our own. The classical examples of these fixed societies are those of the insects, notably the ants, bees, and termites. In these societies, there is often a rigid caste system, each individual being largely restricted to certain duties such as fighting, gathering food, or reproduction. The most extreme example of this is perhaps the beehive, where division of labor is extremely complex. Only one female, the queen, is capable of reproduction. The males, or drones, are of no value to the colony except for fertilization of the queen, and they are driven away eventually by the workers of the hive, which are sterile females and which perform all the essential duties of the colony. During the summer they gather food and store it for the long winter. Certain individuals sit at the entrance to the hive and air-condition the interior with buzzing wings. In winter, the bees are active enough to keep the hive above freezing, although they are doing nothing except producing heat. The life of each individual is completely subordinated to the life of the group.

Such control of behavior is not brought about by external laws, as would be necessary if a human society of like nature were to be formed. Instinct governs all matters in the lives of these animals, and the concept of individual liberty, which has been so important in human life, has no place in their societies. For this reason the student of human populations is likely to find more rewarding the study of less stereotyped societies, especially those of such higher animals as birds and mammals.

In these societies, there are many similarities to our own, though without the basis of law, which is so important to us. Almost every animal society, in these higher groups, has a hierarchical order, with leaders and followers. Those near the top of the order are dominant over all those below them. Since this phenomenon has been studied extensively in birds, where dominance is expressed by pecking, it has been spoken of as the *peck order*, but it occurs in other groups besides birds. Unlike some human societies, these social orders permit an individual to improve his status in the social order under certain circumstances. It is, however, extremely difficult to do so, for in addition to the physical inferiority which largely controls the peck order, psychological factors apparently play an important part. An individual near the lower end of the scale may grow to be physically capable of dominating some individuals at higher levels, but long periods of deferring to these animals evidently instill a feeling of inferiority which may prevent him from assuming a higher place in the social order.

Physical ability may also have much to do with the reproductive success of the individual in colonial species, or in those individuals who gather together during the breeding season. The older and stronger males may gather around them all of the available females, successfully driving off weaker males who are quite capable of breeding. This occurs in seals and in many other polygamous animals which form breeding aggregations.

Although man has been long considered a creature apart, biologists have recently come to suspect that human societies, though based to some degree on intelligent cooperation, may be subject to some of the controlling factors which act on animal societies. Many feel that a clear understanding of the structure, functions, and limitations of animal societies will help us in understanding human social problems. As an example of this, Calhoun (1952) pointed out that in a society of Norway rats, with abundant feed but limited space, the population became stabilized at a level well below that which would have resulted in starvation, apparently due to the direct and indirect results of intraspecific strife. In view of the rapidly rising human population and the rapidly shrinking space per person, students of population dynamics may well ponder the question which this study brings out: Will the human population level off at a point well below the starvation level, or will the numbers continue to rise until population outruns subsistence?

Laboratory biologists have studied the growth, development, and decline of populations under controlled conditions in an attempt to ascribe causes to the various phenomena which have been observed in nature. Such studies should lead to more critical field studies, although it is difficult to determine causes in the field when so many factors are uncontrolled. Nonetheless, much can be learned which will aid in the interpretation of laboratory results, and, conversely, many phenomena will be noted which may be further explained by later work in the laboratory. The importance of such studies is well expressed by Calhoun (1952): "We must have the courage and foresight to depart from the laboratory in its customarily accepted sense, and take with us into the broader laboratory of field situations our extensive knowledge derived from analytical studies of the individual and small groups."

It is necessary for the field biologist to understand and utilize the modern concepts of population dynamics which have been discussed in this chapter. We have been able to give only hints of the currently fruitful avenues of research in this rapidly expanding field, but the interested student will find a great deal more information in the references listed below.

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chapter 10

Animal behavior

Science is not, as some think, like a vast parade of soldiers with a broad front, advancing in lockstep to the lively music of logic. More nearly, science is like an army in combat. Now a squad on the left breaks through an enemy strong point and the whole flank, exploiting its opportunity, advances. But it advances only a little way before it either hits new, stronger enemy positions or threatens to get out of reach of its supply and communication lines from the rest of the army. So the whole front advances in a totally unpredictable and irregular fashion, yet each squad, as it were, is dependent upon all the rest.

The study of behavior is a case in point. This particular "squad" has been advancing rapidly for several decades. At times it has seemed to outreach its supply and communication lines. Indeed, arguments have often arisen within the squad as to the direction of advance, the position of the enemy, and the advisability of continuing along current lines of attack.

Beware instinct . . . instinct is a great matter.

Shakespeare, "King Henry IV." Part 1, Act II, Scene 4

Fortunately, other sectors have also been advancing rapidly, and the breakthrough is still being exploited with the publication of papers and books, the establishment of centers for behavioral research, and the origination of several journals to handle the output of behavioral scientists. In this chapter we shall attempt a brief review of this large and expanding field, particularly as it relates to the field biologist and his interests.

Man's close association with and dependence on animals made their behavior a matter of intense interest to primitive humans; and where primitive hunting cultures exist today, this subject is still an essential part of the education of every young man. The drawings found in caves occupied by early humans and the similar kind of art common to contemporary primitive cultures indicate the importance of animals in the lives of these hunters. They also indicate a sharpness of observation which suggests that primitive peoples knew, and know, a great deal about animals. Such knowledge is necessary to survival. Whether it is the Eskimo, stalking the seal and walrus in the frozen wastes of the arctic, or the Aboriginal, tracking the wallaby in the bush country of Australia, the problem of understanding animals is a very important one.

In our culture, knowledge of animal behavior is rarely a matter of life and death, except to big-game hunters. But it has great interest to sportsmen and nature lovers, as well as to biologists. The biologist's interest in behavior may be a purely scientific one, but the fruits of his labor are useful in many ways. To the taxonomist, behavior may be significant evidence about the evolutionary relationships of certain groups in which the morphological evidence is not clear-cut. For example, Lorenz (1941) revised the classification of the dabbling ducks largely on the basis of their courtship behavior. To the wildlife biologist, knowledge of animal behavior is a basic necessity for intelligent management. The quail, which lives in coveys in the open field, must be managed in a different manner from the ruffed grouse, which lives a more solitary life in the forests. The psychologist, the anatomist, the physiologist, all profit in their respective fields from a knowledge of behavior.

It may be well to begin our discussion of animal behavior with a few definitions, so that the terms we are to use in subsequent pages will be clear and familiar. We must first settle on a definition for behavior. Emlen (1955) defined behavior as "the means by which an animal maintains its relation with the environment," thus stressing the functional importance of behavior. This definition immediately appeals to the field biologist because of its recognition of the environment, but it can be stated more simply that behavior *includes all the acts performed by an animal.* Whether an animal is eating, sleeping, fighting, or mating, its activities are a part of its behavior. It is an animal's way of reacting to its environment.

Causes of Behavior

Behavior is caused by various things within or around the animal which stimulate it to action. These causal agents are called *stimuli.* A stimulus which comes from outside the animal, and which the animal can perceive only through the external sense organs, is an external stimulus. It is something which the animal can see, hear, smell, taste, or feel. The approach of friend or foe, the smell of prey, the falling darkness, or the approaching daybreak—all these and many more may influence behavior.

Other stimuli are internal, resulting from changes in the physiology of the animal. Most such stimuli are brought about by the release into the blood stream of powerful chemicals known as hormones, secreted by the various endocrine glands of the body. Fear, anger, hunger, sexual desire may cause internal activity which will result in a particular type of behavior. It can be seen, then, that the two types of stimuli are not separate phenomena, but that they work together to control the animal's behavior. An external stimulus, in the form of a potential mate, may bring about increased hormonal activity within an animal, leading to courtship behavior. Indeed, it is often difficult to determine the type of stimulus which has caused a particular kind of behavior. We know that most dogs hunt, but the cause is not always clear. A dog may hunt because he is hungry (an internal stimulus only); or because he sees a rabbit, even though he has just eaten (the rabbit being an external stimulus which no doubt causes internal changes as well); or, in the absence of either prey or hunger, because of some internal stimulus which causes predatory animals to go through the actions of hunting even when they are well fed. Furthermore, the particular manner in which the dog hunts represents part of his behavior and varies among the various breeds of dogs.

Types of Behavior

We cannot, then, categorize behavior on the basis of the stimulus which causes it. Some other criteria must be devised which can be readily distinguished. For many years, biologists have categorized behavior as *instinctive* (also called innate, native, or unlearned) and *learned*. Instinctive behavior has been defined as *behavior which is determined by genetical factors and is unmodifiable by circumstances of the environment*. Learned behavior, on the other hand, may be defined as *behavior which is developed as a result of experience*.

Although this distinction sounds clear enough, it is not always easy to apply. The student who is observing an animal, especially in the field, cannot know all the details of that animal's past history and thus cannot always tell whether or not a given behavioral act has been learned. Reiss (1950) has suggested three criteria for determining whether given behavior is instinctive or learned. First, the trait must occur in all members of a given species (allowing for differences in sex, in castes of social animals, and so forth). Second, it must occur independently of the cultural or social environment of the individual. Third, it must occur spontaneously in an animal which, before the trait appeared, had been separated from other members of his own species.

Some instinctive traits can thus be easily recognized. Juvenile red-backed mice (*Clethrionomys gapperi*) are born blind, and the eyes do not open until about nine to twelve days of age. Before this time, they gain a reasonable degree of equilibrium and make a good deal of noise. If disturbed in the nest, an active young mouse whose eyes are not yet open may sit up on his haunches and box at the disturbing influence with his front paws. Since he has never seen this done, it seems quite certain that such behavior is instinctive. After the eyes are open, or in the case of newly captured adult animals, the approach of a potential enemy will cause the mouse to poke its nose cautiously through the top of the nest to sniff and peer around. This activity may be the result of learning, perhaps even the result of captivity. Without careful experimentation, it is impossible to know.

Prenatal Learning

Another difficulty in the recognition of instinctive behavior is the fact that some learning occurs during prenatal or embryonic stages. Such behavior can only be recognized after intensive study of the development of each species, and such studies have been made for only a few animals. Kuo (1932) concluded that the pecking motion of the chick, which had been thought to be instinctive, was actually learned by a series of neck-stretching exercises which take place as the embryo develops, probably beginning as reflexes. Probably many acts now thought to be instinctive will be found to fall into this category.

Reflexes

Some behavioral acts, based on a particular arrangement of muscles and nerves, are called reflexes. A *reflex act* is always elicited by a particular stimulus and never without such a stimulus. A simple reflex is innate in the sense of being built into the body organization of the animal, but behaviorists do not consider a reflex to be synonymous with an instinctive act. A *conditioned reflex* is learned, and results from association of a particular stimulus with a particular event. Pavlov, the Russian physiologist who discovered this type of reflex, was able to induce secretion of saliva in dogs by ringing a bell. The conditioned reflex developed after repeated occasions on which Pavlov rang the bell while food was offered to the dogs.

Since animal behavior is affected by the animal's embryonic development, by its anatomy and physiology, as well as by the more obvious environmental causes, study of animal behavior may be approached from several directions. In general, three approaches have proved most fruitful. Psychologists study learning and learned behavior; physiologists and anatomists cooperate in studying the structure and function of the nervous and endocrine systems and their relationship to behavior; and ethologists observe and study behavioral patterns, placing particular emphasis on instinctive behavior.

Psychological Study of Behavior

Perhaps the largest group of behavioral scientists in the United States has been the psychologists, though the other two approaches have not lacked for adherents. Psychologists have been concerned with the methods of learning and with studies of the learning ability of various species, including man. Such work must of necessity be done in the laboratory with captive or at least tamed animals and with elaborate experimental setups. Most of the work in animal psychology has therefore been done on a few specially well-adapted species. The rat, the chimpanzee, the domestic pigeon, the dog, the chicken, and man himself have been extensively studied.

In general, psychological behaviorists are hopeful of learning something about man by the study of lower organisms. For example, the extensive and stimulating work by Harlow (1962 and many other papers) on the affectional development of Rhesus monkeys has obvious significance to those attempting to rear children. These same facts, however, are of value to the field biologist in interpreting the behavior of animals under natural conditions. Similarly, the field study of animals may help the laboratory psychologist to interpret his observations, and Schneirla (1950) has pointed out the desirability of introducing the methods of animal psychology into field work to supplement laboratory studies. Similarly, studies in physiology and anatomy are basic to an accurate understanding of psychological phenomena, but are often neglected by psychologists. Hebb (1958) has commented on this problem from the point of view of a psychologist.

Physiological-Anatomical Study of Behavior

The real secrets of behavior are, of course, locked within the body of the animal itself. The nervous and endocrine systems which are responsible for the physical and chemical coordination of body activities have been the subject of intensive research by students of behavior with a background in physiology and anatomy. Modern electronic, biochemical, and physical techniques have brought about rapid advances in these areas (see Harlow and Woolsey, 1958), and some of the finest and most sophisticated experiments are being done by physiologists interested in behavior. Most heartening of all, some physiologists are integrating laboratory and field studies successfully in the study of behavior. Swihart (1963) for example, has studied the behavioral patterns of some tropical butterflies. By coupling careful electronic studies in the laboratory with careful field observation, he has been able to show the relationship between electrical patterns in the nervous system of the butterfly and behavioral patterns which occur rhythmically in the field or in large cages.

Ethological Study of Behavior

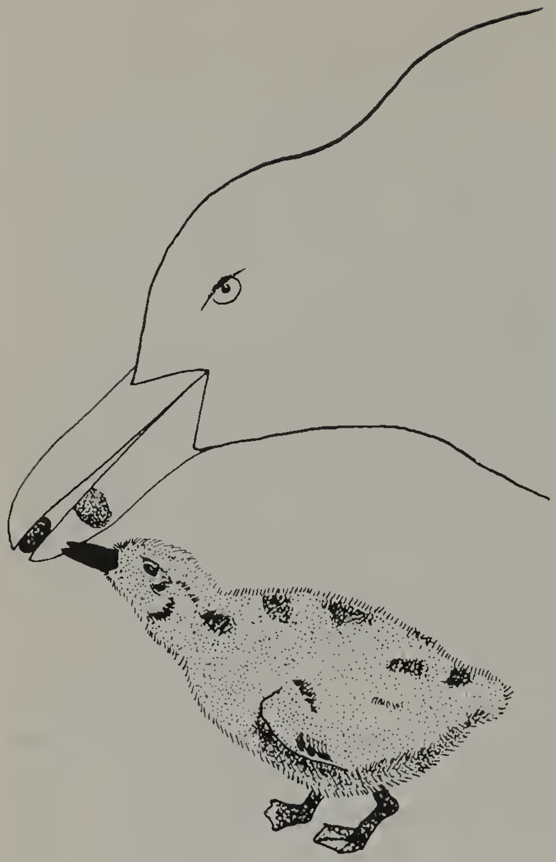
Despite such studies and more general integrative works such as the short book by Dethier and Stellar (1961), the full integration of field and laboratory studies of behavioral phenomena remains an aim rather than a fact. From the point of view of the field biologist, the development during the late 1930s and early 1940s of a group of students of instinct has become the most exciting aspect of behavioral study. This group of biologists, which has developed largely in Europe, approaches the subject from the standpoint of behavior under natural conditions, and with particular stress on instinct. Uncontrolled field conditions often lead the observer to an idea which can then be experimentally checked, and study of behavior in this way has come to be known as *ethology*. The ethologist emphasizes study of the act in itself along with the patterns of acts associated with a particular aspect of the animal's life in an attempt to discover external stimuli which bring about the behavior being explored and to deduce something about the underlying mechanisms and the manner in which they function. Since this is the approach to behavior which is most widely used by field biologists, and since it is the center of much research and some controversy, the concepts and terms of ethology will require definition and explanation.

The Releaser Concept. Animals, according to leading ethologists, are born with certain predetermined (innate) behavior patterns which are of genetic origin. Their appearance may depend upon the proper conjunction of the proper stimuli or the development of the animal to a specific age, but the patterns are "genetically coded" (Thorpe, 1954) and are constant for a particular species. These innate or instinctive behavior patterns may be distinguished from reflexes, however, in that *they are not always dependent upon a specific stimulus.* Ordinarily they result from a particular kind of stimulus which is highly specific, just as a reflex does. This kind of stimulus—a property of the stimulating object which can affect the external sense organs of the receiving animal—is called a *releaser.* An example may help to clarify the meaning of this term.

Young herring gulls are fed by their parents when they peck at the tip of the parent's beak. Tinbergen (1949) has shown that the young birds respond with the begging reaction not to the beak or to the parent but to a red spot prominently situated near the end of the lower mandible (Fig. 10-1). By the use of models, Tinbergen was able to prove that a red spot, in the same position as that on the parent's beak, was the most effective releaser for this activity. Spots of other colors were less effective, and a bill without a spot brought about begging activity in only a few individuals. Changes in the color of the bill and head indicated that these characteristics were not important in eliciting the reaction, but that the red spot was the releaser of the food-seeking reaction.

Other releasers may bring about sexual behavior, e.g., the red coloration of certain male fishes during the breeding season; nesting behavior in birds, e.g., the shape and coloration of eggs; and any other aspect of an animal's inherited activity pattern. Indeed, some students of behavior believe that all social aspects of instinctive behavior, that is, those concerned with another member of the species, and many nonsocial activities as well, are controlled by releasers.

Thus far, an instinctive reaction set off by a releaser does not seem to be different from the previously mentioned reflex. Some years ago, a school of behaviorists held that *all* behavior is made up of reflexes. Instinctive reactions, however, have one peculiarity which separates them from reflexes. If the



Redrawn from Tinbergen, 1951

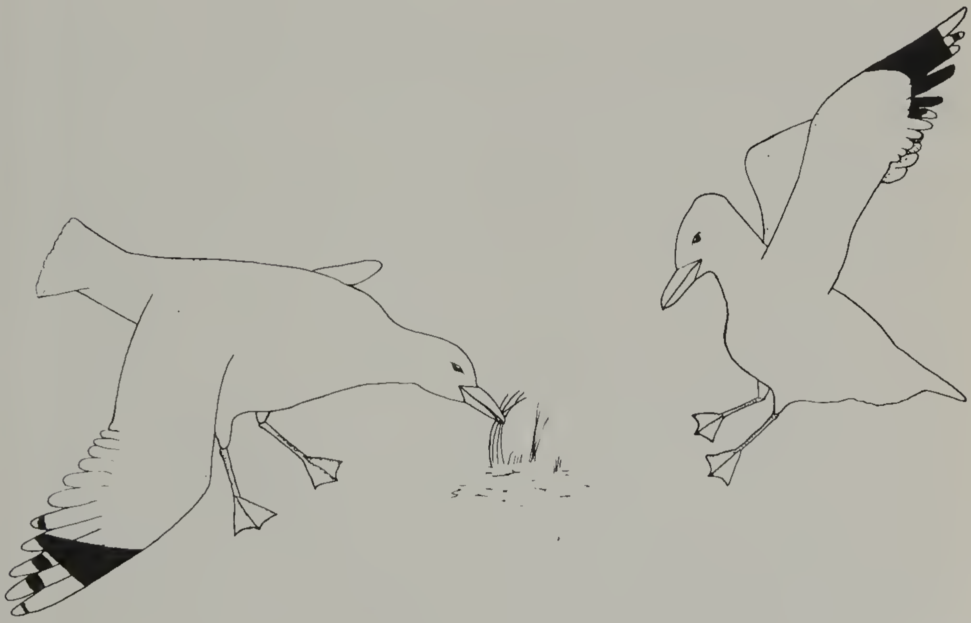
Fig. 10-1 The red spot on the lower mandible of the herring gull's beak releases the pecking activity of the chick.

releaser for a particular act does not appear for long periods, a normally inadequate stimulus may cause the act to be performed; or in some cases it may be performed with no recognizable stimulus. Lorenz (1935) coined the word *Leerlaufreaktion* for this phenomenon. Tinbergen (1951) has rendered this in English as "going off in a vacuum."

This peculiar fact has caused ethologists to suggest the existence of some specific structure controlling each instinctive reaction. These postulated structures are called *innate releasing mechanisms* (IRM's). When the proper stimulus occurs, it is believed that the IRM which is affected by it permits nervous energy to flow through the proper channels and to bring about the specific act which is elicited by this stimulus. When the act is long deferred, because of a lack of the stimulus, it is postulated that reaction-specific energy is built up in the nervous system. If this energy continues to be built up and the releaser for the IRM which blocks its discharge does not appear, the reaction-specific energy may overflow the IRM and be discharged as a *Leerlaufreaktion*. A captive bird, for example, may perform such complex behavior as the courtship behavior, or catching, killing, and eating imaginary insects, even though the usual stimulus is absent.

Displacement Behavior. Occasionally a bird reacts to obvious stimuli with a type of behavior which has no apparent relationship to the stimuli and which is completely unsuitable to the circumstances. This is called *displacement behavior*, and is believed to indicate a conflict between two opposing drives caused by different stimuli. Unable to decide upon a course of action, the animal may perform some quite unrelated act.

When two birds are fighting, one may suddenly abandon the fight and perform some unrelated act, such as picking at food or preening the feathers (Fig. 10-2). In such a situation, it is suggested that the bird is stimulated to fight and stimulated to flee, with the result that it does neither. Tinbergen (1951) has indicated that displacement behavior may also occur when a drive such as the sexual drive is particularly strong but the external stimuli necessary for its release are missing. When



Redrawn from Tinbergen, 1951

Fig. 10-2 Displacement activity in the herring gull. The bird on the left is reacting to aggressive behavior by gathering nesting material. See explanation in text.

a male animal is attempting to mate with an unresponsive female, he may turn, in what seems to our minds to be frustration, to some completely unrelated activity. The slightest encouragement from the female, however, is likely to result in resumption of the courtship by the male.

Imprinting. Some peculiar reactions of animals defied explanation until modern ethologists recognized the process known as *imprinting.* At a certain stage in the life of an animal, a particular stimulus may fix, in that animal's behavior pattern, a certain reaction. This reaction will, for the life of that individual, or at least for long periods, result whenever the stimulus which first elicited it is present. This same stimulus will have no effect on other individuals of the same species unless they too have been subjected to it at the appropriate time. *This shows that the imprinted reaction is learned rather than innate,* although it may well depend on some innate mechanism which is acted upon during the imprinting process. The readiness of newly born or hatched animals to accept a foster parent, even of a different species, results from this phenomenon. At a certain age, which varies in different species, any object which meets certain rather specific requirements will be accepted as a parent and will be followed with unshakable devotion so long as the young animal has any need of parental relationships. Ramsay and Hess (1954) have shown that a newly hatched mallard duckling will accept as its parent anything which comes within its range of hearing making a ducklike quack. Obviously, under natural circumstances, this is almost certain to be its mother, so the mechanism is more or less foolproof. But if another duck, or other object making a similar noise, is introduced to it at the proper stage, that object will be accepted and followed until the duckling reaches the age of independence. This phenomenon explains the many cases of domesticated animals which appear to regard a human as their parent. It is common for pet owners to say, "My dog thinks he's a person," or some such statement. Actually, of course, the dog is not thinking any such thing. He is simply reacting to people as though they were members of the same species. Lorenz (1952), in an amusing and instructive book, tells of his experiences with animals of several species which he taught to regard him as a parent or species mate.

Imprinting may be accomplished by auditory stimuli, visual stimuli, or by other means. The fact that such a phenomenon exists explains the difficulty of training or taming an animal if it has reached a certain critical age before it is approached (Hess, 1958).

Reaction Chains. The examples we have given thus far have been concerned with relatively simple and specific reactions. Many social activities of animals, however, follow a regular and complex pattern of events. Each act of one individual leads to another act by the other. This in turn releases another activity of the first individual, and so on. Such a *reaction chain* is perhaps best typified by the courtship and mating behavior of certain animals. An example is offered by the courtship of the three-spined stickleback as described by Tinbergen (1952).

The male stickleback builds a nest on the bottom of the pond and waits nearby for a female to appear. When a female with a swollen abdomen, indicative of breeding condition, approaches the territory of the male, he commences a zigzag movement which shows off his red underside to advantage. If the female is ready to mate, she responds by swimming directly at the male. He then turns and swims rapidly toward the previously constructed nest. The female, evidently attracted by this movement, follows him, and he puts his head into the nest entrance. This invitation encourages the female to enter the nest, and when she has done so, the male begins a quivering movement. The female then begins to spawn, whereupon the male sheds his sperms over the newly laid eggs. These reactions are shown diagrammatically in Fig. 10-3.

The complexity of such reaction chains is important in preventing the mating of individuals of closely related species which might be genetically compatible. Although hybridization does occur in nature (see p. 52), it is usually between

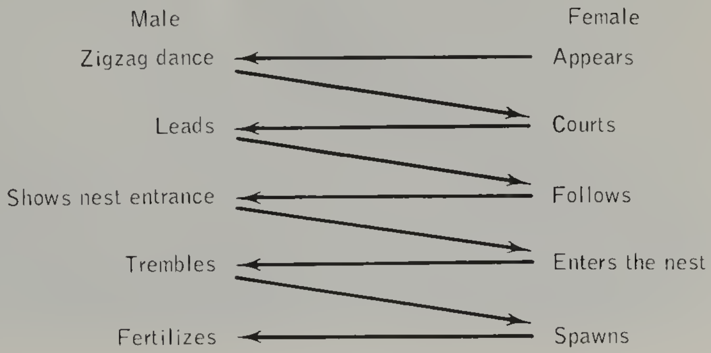
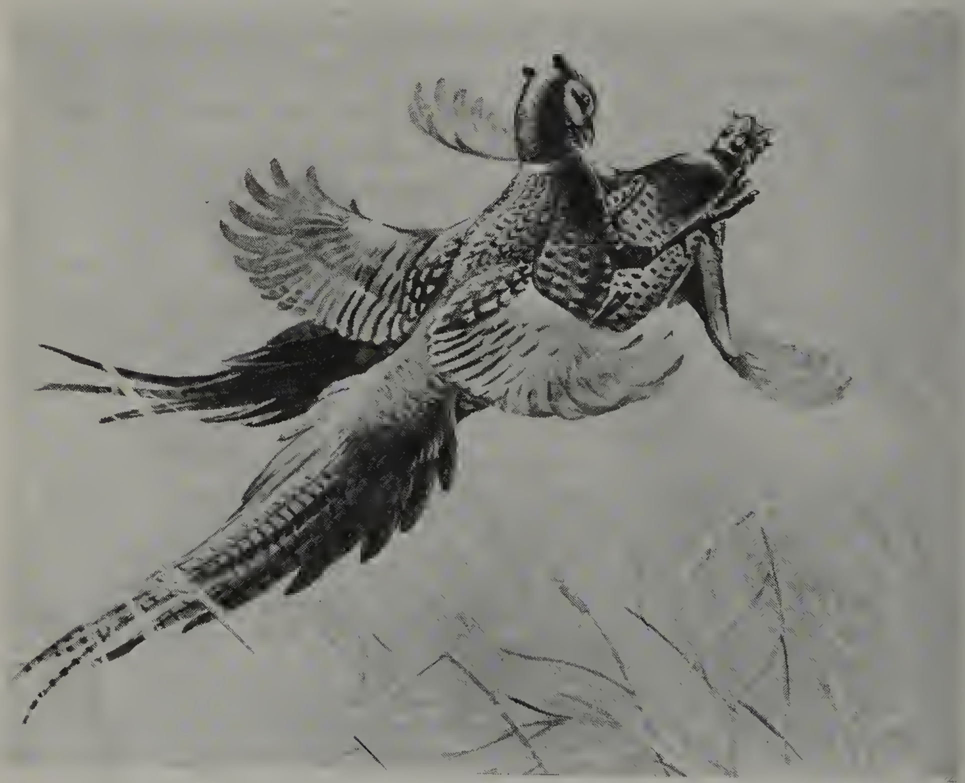


Fig. 10-3 Mating activities of the three-spined stickleback. Reproduced from Tinbergen (1951) by permission of the author and Oxford University Press.

species whose courtship pattern is similar. Otherwise the activity would be broken off before the actual mating occurred.

At the end of every reaction chain, or as a result of each instinctive act, an event occurs which satisfies the animal's immediate need. Thus the courtship behavior described above results in the laying and fertilization of eggs. Fighting behavior results in the defeat of one individual, which seems to satisfy both. These final acts of a chain, such as coition, eating, or flight, were called by Craig (1918) *consummatory acts.*

In most cases, these consummatory acts have been preceded by other activities which Craig called *appetitive behavior*—behavior which puts the animal in a position or state favorable to the satisfaction of its needs. Under the influence of stimuli, probably mostly internal, the animal begins the appetitive behavior. It must be stressed that this is done by instinct, not by reasoning. A male bird does not reason that its chances of obtaining a mate will be better if it chooses a

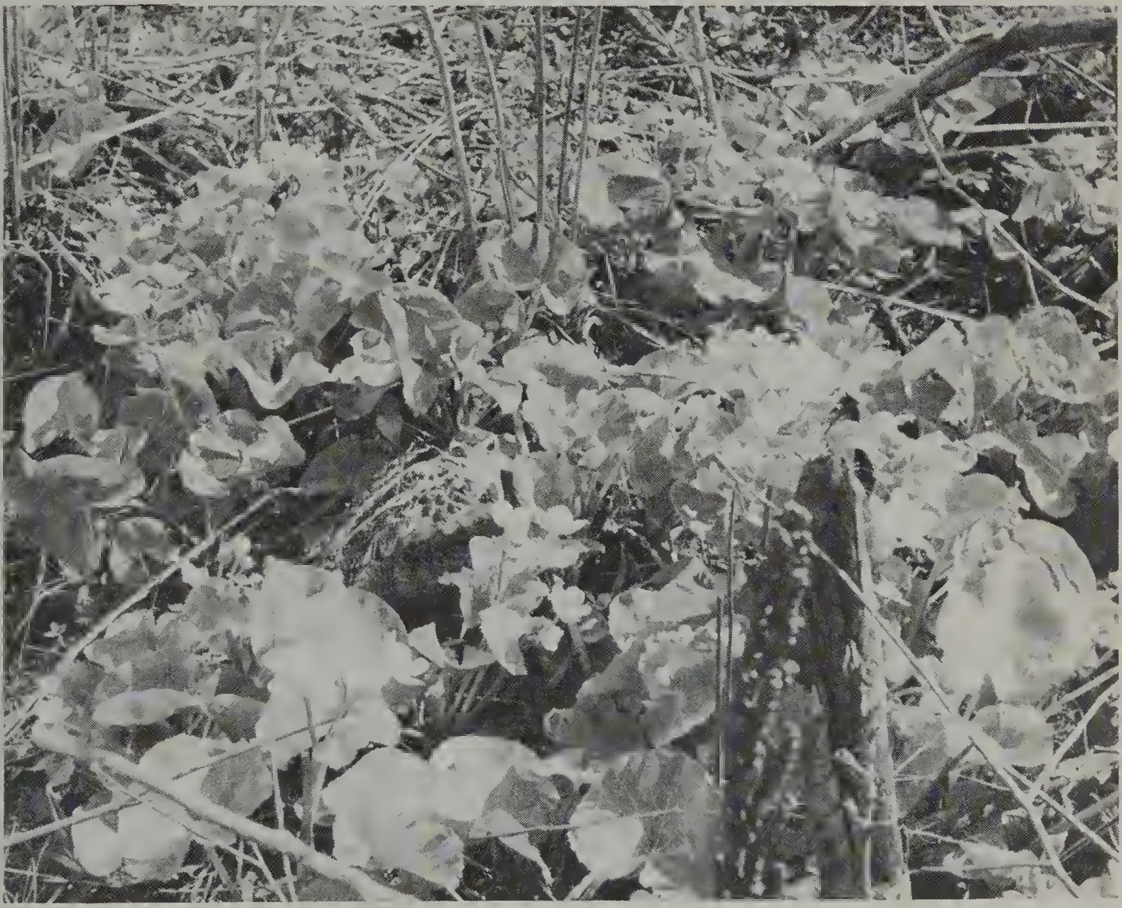


H. Wayne Trimm

Fig. 10-4 Territorial behavior in the ring-necked pheasant: two males fight at the margins of adjacent territories.

high perch and sings loudly. Yet this is the most effective means of advertising his availability and of attracting a female. The male bird is probably unaware of his desire for a mate until her appearance releases the next reaction of courtship. His singing simply announces to others of his species that he has chosen a territory, as well as announces his sexual vigor and readiness for mating.

The Value of Instinct. Instinctive responses to stimuli have a part in every aspect of the animal's life and, particularly, in every relationship with others of its own kind. The sudden onslaught of a bird defending his territory (Fig. 10-4) seems to frighten his opponent and often results in a victory without injury to either animal. The tendency to depend on protective coloration in escaping is evident in some animals, while others, equally well adapted for protection if they remained still, flee

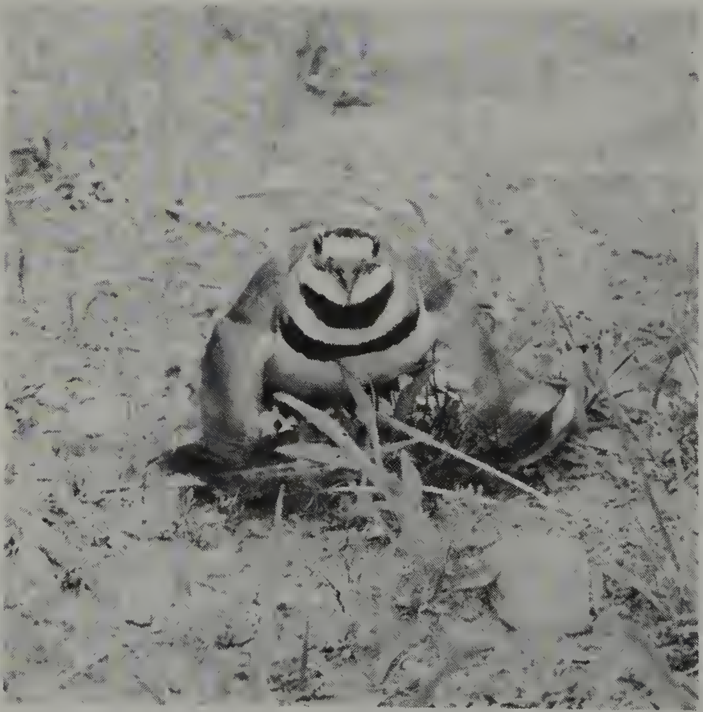


Allen H. Benton

Fig. 10-5 Protectively colored birds, such as the woodcock shown here, often remain on the nest until touched.

at the approach of an enemy. The woodcock (Fig. 10-5) will remain in its hiding place or on its nest until it is almost stepped on and will then rocket away; or, if nesting, will flutter away as though it had been injured. The cottontail rabbit will crouch in its lair until it is almost literally kicked out of it. The killdeer, on the contrary, with protective coloration almost as effective in a field as is that of the woodcock in the swamp, will slip off the nest while the observer is still far distant and attempt to lead him away with a broken-wing act. If this fails to draw the intruder away from the nest, the bird will attack with beating wings and open beak (Fig. 10-6), alternately advancing and retreating until the intruder has been decoyed a safe distance from the nest. At other seasons, killdeers are extremely skittish and often frustrate the bird watcher by taking off with loud cries and causing other normally approachable shore birds to depart before the observer can study them.

The survival value of behavior patterns is also shown in the behavior patterns of subsocial and social animals. It is

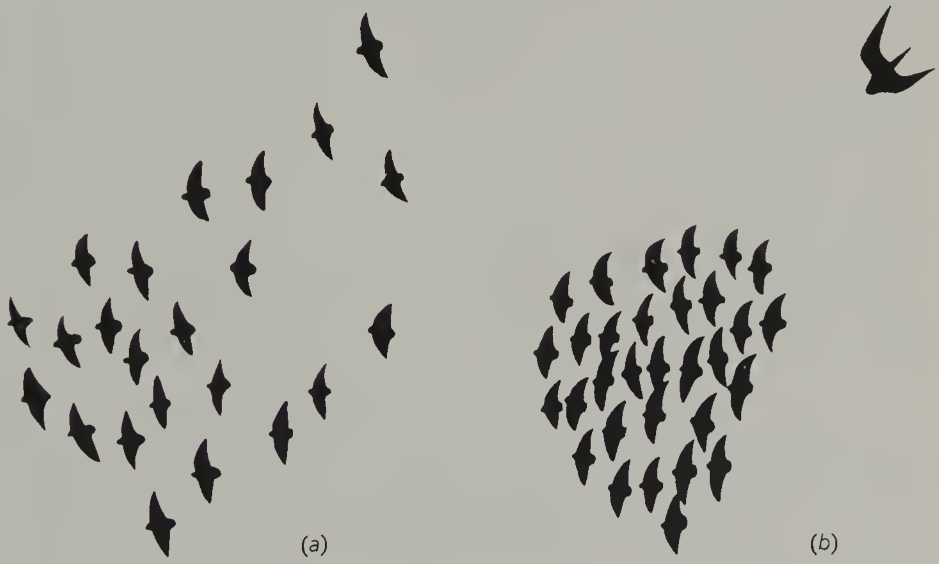


Allen H. Benton

Fig. 10-6 Threat display of a nesting killdeer. After attempting to lead the observer away from the nest by appearing to be injured and by cries of distress, this species will then turn and fly at the intruder if he approaches the nest too closely.

a commonly known fact that bobwhite quail coveys sleep with their heads pointed outward in a circle and that musk oxen, when attacked by predators, form a circle with the females and young inside, and the bulls, with their heads outward, set up a strong barrier of horns. Flocks of starlings normally fly in a loose pattern (Fig. 10-7*a*), but when such flocks in flight are attacked by a hawk they form a tight group, maneuvering as one bird to escape the enemy (Fig. 10-7*b*). Since the hawk cannot attack one starling in such a group without danger of colliding with others, he cannot effectively attack the group, but must follow until one bird gets sufficiently far from the flock to permit assault.

While instinctive behavior is adapted to meet the usual situations which confront an animal, it may at times lead the animal into trouble. Since instinctive responses are not reasoned and do not vary with the circumstances, they are not always suitable. Tinbergen (1951) relates how herring gull chicks instinctively seek shelter when the adult bird gives an alarm call. While he was observing a gull family from a blind, Tinbergen disturbed the adult bird, which gave the alarm call. The chicks, seeking the nearest shelter, ran directly to his blind and crouched at his feet. In this case, of course, no harm was done, but it is obvious that there was no survival value in the response of the chicks in this particular situation.



Redrawn from Tinbergen, 1951

Fig. 10-7 (*a*) Normal flight pattern of the European starling flock. (*b*) Flight pattern of European starling flock attacked by hawk. See discussion in text.

Directive Activity. At the higher levels of animal life, as might be expected, some parts of behavior which are instinctive in lower animals are replaced by *intelligent* or *directive activity.* This is, of course, most noticeable in man and the higher primates, but it occurs in some degree among many other animals. Unless we can prove experimentally, therefore, that a particular activity is performed without reasoning or foresight, we ought not to assume that it is. We can say that in most cases an animal cannot clearly understand its needs or devise a means of satisfying them. Conversely, we must be careful not to attribute intelligent or directive behavior to animals without scientific and experimental evidence to support our contention.

"Humanizing" Animal Behavior. The tendency to attribute human characteristics to animals seems to be a universal one, and this has led men of all times to interpret animal behavior in terms of human emotions. Today this approach results in the use of such terms as "reproachfulness" or "gratitude" with reference to some aspects of animal behavior which quite likely have no relationship to such emotions as we know them. Early settlers in the country had a charming legend about the chimney swift, which illustrates the lengths to which this kind of thinking may be carried. The swifts nest in unused chimneys, building small nests of sticks glued together with saliva and plastered to the walls of the chimney. Since the nests are small and shallow, it often happens that a young swift, before it is able to fly well, falls from the nest and cannot escape back up the chimney. When such birds appeared in the fireplace of a settler's house, it was attributed to gratitude on the part of the parents for the hospitality granted them. The young bird was cast down the chimney, it was believed, as a sort of rent payment for the use of the chimney. Although this may seem absurdly simple-minded to sophisticated modern minds, many of us still apply much the same sort of thinking to our analyses of animal behavior.

This is not meant to imply that animals other than man do not have emotions. Anyone who has seen a dog terrified by a thunderstorm is not likely to doubt that animals experience fear. But we cannot determine the precise emotions of animals with which we cannot communicate, and we therefore have no logical reason to attribute to them emotions similar to our own.

Criticism of the Ethological Approach

The promulgation of new theories by the ethologists has not been entirely without critics within the field of behavior. Indeed, it has received severe criticism by a number of proponents of the psychological and physiological approaches to the study of behavior. Perhaps the most carefully detailed indictment of ethological theory is that of Lehrmann (1953). He pointed out that ethologists were going far beyond the available evidence in their theories, that they were drawing inferences from lower organisms to explain quite different behavioral phenomena in higher organisms, and that their emphasis on the stereotyped character of instinctive traits discouraged inquiry into the actual source and development of the various aspects of behavior.

In their work, however, the ethologists have stimulated a tremendous amount of research, both among their supporters and among their detractors. Whether or not, in the long run, their theoretical framework proves to be generally correct, they have been at least partially responsible for the burst of activity which has characterized the field of behavior since 1940. Out of such controversies comes scientific progress.

Behavior and Ecology

For some years, ecologists remained largely aloof from the behavior controversy, and ecology texts in general ignored the importance of behavior as a factor in the environment. Recently there is evidence that the trend toward integration of varied viewpoints has reached out into the field of ecology. Klopfer (1962) has gone so far as to suggest that the behavioral sciences have much to contribute to the solution of some fundamental problems of ecology. He cogently pointed out that prey-predator relationships are directly connected with the perceptual world (*Umwelt*) of animals, which has been a useful concept in behavioral study; that distribution and abundance are directly related to intraspecific behavior; that communication and communities have more in common than phonetic similarity. The field biologist in search of ideas for study will find that the development of behavioral ecology presents yet another challenging area for research.

Biological Clocks

For many years, biologists have known that some organisms exhibit definite cycles of behavior and activity as though they had some kind of internal clock. Some of these activities can be shown to result from recognition by the animal of obvious cues in the environment, such as light and darkness, changing length of the day, or changes in temperature or humidity. In other cases, however, no such cue has been demonstrated, and the cyclic activity continues even under changed conditions. Marine crabs which have a daily cycle along the East coast have been transported to the Pacific coast. There they demonstrated the same cycle as though they were still on Eastern Standard Time. Planarians, small worms with limited nervous systems, show differential behavior toward certain prey organisms, attacking them only at certain times of day, regardless of light conditions. Many similar cases could be cited, which seem to show that many animals have some means of determining time and assuming a particular type of behavioral activity without regard to external environmental conditions.

What permits such close timing of biological events with occurrences in the environment is as much a mystery as how behavior patterns are coded in the nervous system. Some biologists postulate the existence of an internal timing mechanism, or biological clock. Whether these clocks are built-in and inherent in the physiology of the organism or whether they are based on complex reactions to events in the external environment, no one can say for certain. Brown (1962) suggests that animals can detect and respond to electromagnetic forces of the earth and possibly to cosmic radiation and radio waves. He thus leans toward an external explanation for these phenomena, but equally strong arguments have been adduced for internal regulation. Here, too, is an aspect of behavior of immense interest with the possibility of ingeniously designed experiments in the field and laboratory.

For the field biologist, then, as well as for the laboratory scientist, there still remains much to do in the study of behavior. The bird lover with a feeding tray under the window may learn much concerning the relationships between birds and about their reactions to specific stimuli. The insect collector may emulate the great Fabre and observe the way in which insects solve the problems of life. The patterns of behavior in courtship and mating are unknown for many mammals and birds, and to an even greater degree, for the lower forms of life. Even though the amateur and the beginner may not feel competent to argue the validity of the various theories of behavior, they can contribute to the store of knowledge by observing and describing the behavior patterns of poorly known species. After enough of this basic information is available, a unified theory of animal behavior may become possible.

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chapter 11

Economic field biology

As we saw in the first chapter of this book, field biology is important from an economic point of view. Nearly all of the major groups of plants and animals include at least some species of direct or indirect importance to man. Some field biologists study organisms regardless of their economic value. Frequently their findings are directly useful. Other field biologists work in practical areas such as conservation and management of wildlife, pest control, soil and water management, forestry, agriculture, and medicine, where the primary concern is with matters of immediate economic importance.

Basic and Applied Research

Perhaps it is well to point out here the difference between *basic*, or pure, and *applied* research, for these terms are frequently misunderstood. When the goals of research are strictly economic, the research is said to be applied. To illustrate, certain entomologists, such as those working in

Then, early in June, the adventurers broke through the interminable wastes of dim woodland, and stood on the threshold of the beautiful bluegrass regions of Kentucky; a land of running waters, of groves and glades, of prairies, cane brakes, and stretches of lofty forest. It was teeming with game. The shaggy-maned herds of unwieldy buffalo . . . had beaten out broad roads through the forest, and had furrowed the prairies with trails along which they had travelled for countless generations. The round-horned elk . . . abounded, and like the buffalo travelled in bands not only through the woods but also across the reaches of waving grass land. The deer were extraordinarily numerous, and so were bears, while wolves and panthers were plentiful.

Theodore Roosevelt, "The Winning of the West"

agricultural experiment stations, may attempt to discover an insecticide to control an insect pest doing great damage to crops. The results of this work, if successful, will be of immediate economic use. The work might be called, therefore, applied research. An ecologist might be working on the same species of insect to determine the conditions under which the larvae develop most rapidly. His work may or may not be of economic importance *at the moment.* Such research, conducted without any specific economic viewpoint, is considered basic research, and hence the work of the ecologist and other field biologists is frequently in this category. However, it is likely that the results of basic research will be of economic value at some time in the future. It is impossible, therefore, to distinguish clearly between the two types of research. When Albert Einstein developed the mathematical formula $E = mc^2$, his work had no practical importance, and he was motivated by no desire to achieve any immediate practical end. Yet when the work on atomic energy was turned toward the development of an atomic bomb, this formula became tremendously important, and its value has perhaps not yet been fully exploited. In biology, similarly, basic research is usually important to other workers in applied science.

Much applied research is carried out by field biologists, and this economically important work will constitute the major subject matter of this chapter. Most of the biologists who do applied research are connected with state and Federal departments concerned with wildlife management, conservation services, forestry, and agriculture, or they are teachers in departments dealing with these subjects in our universities. They are interested in the control of pests and injurious plants and animals and in the conservation of our food resources, soil, water, forests, fish, and game.

CONTROL OF PEST SPECIES

One of the greatest problems confronting agriculture is that of losses due to insect pests. In the United States, the losses in one year as the result of the depredations of more than 600 injurious insect species amount to about 4 billion dollars (Haeussler, 1952). This staggering sum assumes special importance when we recognize that it represents the fertility of American soil, which produced the food consumed by the insects.

The control of these pests is not easy, largely because there are so many kinds of them. There are more species of insects than there are of all other kinds of animals put together. This variation is accompanied by equally great variation in life habits, so that it is impossible to deal with all insects in the same way. An insecticide effective against one species may be totally useless against another, or it may be effective at certain periods of the life cycle and not at others. Furthermore, some insects are beneficial. We do not want to kill them along with the pests or do damage to other valuable animals and plants. It is easily seen, then, that the problem of insect control is ecological in nature. An insect pest must be studied to discover what kinds of foods it eats, when it breeds, when the low points in its population occur and why, its natural enemies, its susceptibility to various kinds of poisons, its activities at all stages of its life cycle, its range and the factors limiting its range, and all the other facets of its life which the other chapters of this book discuss. It should also be noted whether the insect makes any beneficial contributions, such as the control of other pests.

Chemical Control of Insects

In recent years, many new chemicals have been developed as insecticides against agricultural pests as well as against medically important insects (see p. 361). In some cases the insecticides are ignorantly or carelessly used, and often organisms other than the intended insect pests are killed. As a protest against this misuse of insecticides, Rachel Carson wrote "Silent Spring" (1962). Many who are not ecologists have commented heatedly on the book, some favorably, some unfavorably. For examples of opposing views on the insecticide problem by a biochemist and a vegetation analyst, see Jukes (1963) and Egler (1964).

In a review of Carson's book, Cole (1962), an ecologist, explains why the problem of pest control is extremely complex and requires solution on an ecological basis. Most of those who use pesticides are not ecologists, nor are they aware of the profound changes in the ecosystem which will occur through the misuse or overuse of chemicals. Insecticides are effective, efficient, and easy to apply. They are important and necessary as an aid in agriculture. However, more research is needed to find selective poisons which will kill *only* the pest species. This is especially true where the area to be sprayed is a forest or some other community containing many species. The sea lamprey investigations are an example of what can and should be done in finding a specific pesticide (see p. 358). For crops, where the community is artificial and simple, a broad spectrum insecticide may be used safely when proper precautions are taken. However, research in the field on the toxicity of various insecticides to different kinds of wildlife has shown that extreme care must be taken in *any* use of pesticides in the environment (Anon., 1963*a*).

Unfortunately, in the past, chemicals have in some cases been applied to insect control without prior and thorough field study of their effects. One serious consequence of such activity is often the increase of another pest as serious as the first. Attempts to control the larva of the codling moth (the apple worm) with DDT resulted, in some areas, in an increase of a pest called the two-spotted mite. The codling moth larva ruins the fruit, while the two-spotted mite destroys the foliage.

Before the advent of DDT, codling moths were becoming more and more resistant to other insecticides, although there was no serious problem with the mites. Soon after the DDT was introduced, codling moths were well under control, but the two-spotted mite had increased to the point where it was an important pest. Apparently the DDT was not only effective in destroying the codling moth, but it was also killing the natural enemies of the mite. A thorough study of the moth and its associates in the apple tree microcommunity might have prevented the occurrence of such an unhappy event.

Biological Control

The use of natural predators, parasites, or disease to control pest organisms is known as biological control (see p. 6). Biological controls are often difficult to find or to use. Also, if a biological control is a predator, such as the praying mantis, it often has a feature common to many insecticides—namely, it is indiscriminate in its attack on insects. Moreover, predators may not by themselves control their prey populations (see p. 387). Still, organisms have been used to control pests in several instances. In one well-known example, insects were used to control a noxious plant, the Klamath weed, *Hypericum perforatum* (Huffaker, 1951). Conversely, plants (fungi) have been used in the control of insects. A familiar pest to many people, particularly in the eastern United States, is the Japanese beetle, *Popillia japonica*. This insect does extensive damage to various kinds of plants (Fig. 11-1), and its larvae may do extremely serious damage in turf on lawns and golf courses. Various methods of control were tried soon after its arrival in this country around 1916, in hope of suppressing it before it could spread. Its life history was studied in great detail in order to find ways in which it could be controlled effectively. The beetle was not a major pest in Japan, where it had several natural enemies. Some 49 of its insect parasites and predators were studied in the hope that they would provide a biological control in this country (Hadley and Fleming, 1952).

Of all the natural enemies that the beetle had in the Orient, only a few proved to be effective or desirable in this country. One of the imports was the red-eyed fly, *Centeter cinerea*, a parasite. It failed to be fully effective here because in the United States it emerged two to three weeks before the maximum emergence of the Japanese beetle. Other parasites

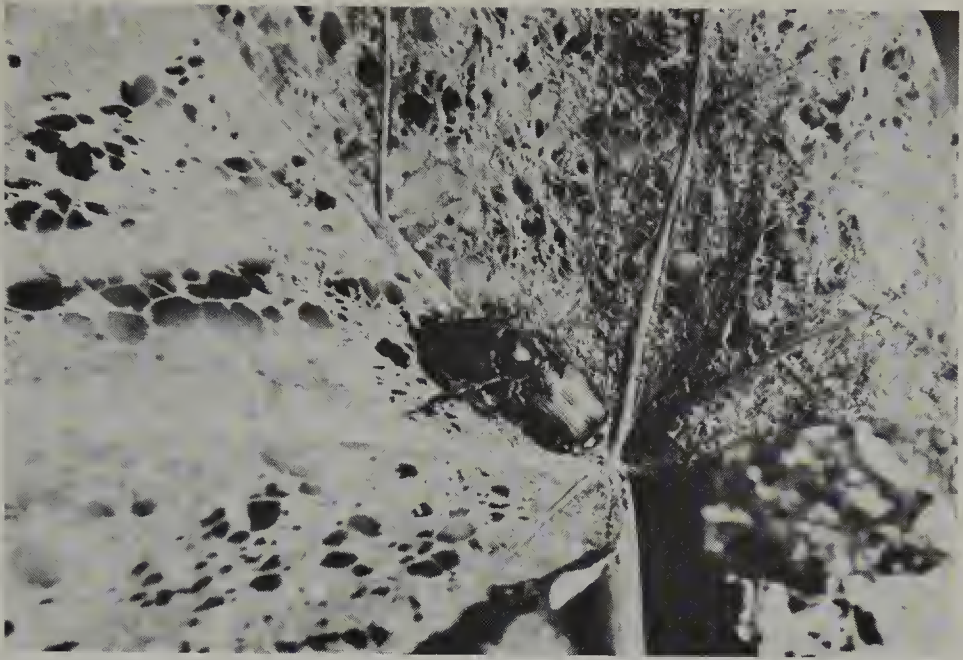

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Fig. 11-1 Japanese beetles, *Popillia japonica,* on grape leaves; this introduced species has become a major pest in the East.

such as *Dexia ventralis* also proved unsatisfactory because they require more than one host species to complete their life cycle. The most important parasites of this beetle in its native land are two species of parasitic wasps, *Tiphia popilliavora* and *Tiphia vernalis.* They have proved to be effective in reducing the beetle population wherever the wasps have been established.

In searching for all the possible enemies of the Japanese beetle, another type of biological control was then developed. Among the organisms producing diseases in this Oriental pest are two species of bacteria, now called *Bacillus popilliae* and *Bacillus lentimorbus.* They cause maladies known as Type *A* and Type *B* milky disease. These bacteria, particularly Type *A*, were found to be effective in killing the larvae of the beetle. In order to obtain spores of the bacteria for use in control of the beetle, it was found necessary to use live Japanese beetle larvae as the culture medium, since usable artificial media could not be found (Hawley, 1952). The spores produced in this manner may be broadcast over areas of beetle infestation, where the milky disease will in time be disseminated throughout the beetle population. Although this type of control may take several years to be fully effective, it is apparently safe in that it is not harmful to other organisms except for a few species of American beetles. Furthermore, one application is good for an indefinite number of years, although the necessary manner of culture makes it a costly control.

Other Control Methods

In addition to biological controls, quarantine of infected areas, chemical controls, and traps have been used in an attempt to restrain the Japanese beetle. Quarantine, as in many other cases, did not prove effective in preventing its dispersal. Several chemicals, including DDT, have been used successfully against it, but of course they will kill beneficial forms as well. Traps are not so useful in decimating the beetle population as they are in surveying areas for possible new infestations. All of these methods, directed against one of the many insect pests in this country, serve to indicate how full biological knowledge is needed for the control of noxious insects.

The Sea Lamprey Problem

Unfortunately, biologists are sometimes called in too late to prevent economic disaster. Such is the case with the marine lamprey problem in the Great Lakes. The lamprey is a parasite which often kills fishes which are its hosts. It attaches itself to the abdominal region of the fish by its mouth disk, rasping its way through the tissue and living on the flesh and fluid of its host. This particular species, *Petromyzon marinus*, is typically a salt-water form but is *anadromous;* that is, the adults enter fresh-water streams to spawn. They require a gravelly bottom to make their nests and lay their eggs. Sea lampreys were able to gain access to Lake Ontario without the aid of man but were stopped from further extension of range by the Niagara Falls. With the completion of the Welland Canal in 1824, they were able to pass into Lake Erie (Hubbs and Lagler, 1958), and no effort was made to stop this emigration. The spread across Lake Erie was relatively slow, perhaps due to lack of suitable streams for spawning. When the sea lampreys finally reached Lake Huron, they spread very quickly throughout the remaining Great Lakes and rapidly reduced the fish populations, especially that of the lake trout. So great was this reduction that the fishing industry suffered severely. In 1941, the total catch of lake trout in all the Great Lakes was 15 million pounds. In 1961, the catch was only 384 thousand pounds (Power, 1963).

Biologists were commissioned to find a way to control the lamprey. Various weirs and other devices are used to trap the spawning adults as they attempt to enter tributary streams. It is evident that in such large lakes as the Great Lakes this is a stupendous task, yet there is no doubt that the spawning season is the most vulnerable portion of their life cycle. Over four thousand chemicals were also tested in order to find a selective sea lamprey larvicide (Applegate et al., 1957). Several suitable poisons were found and have been applied. This tremendous research effort appears to be successful, since in Lake Superior, lamprey counts in 1962 were down 80 to 90 per cent of the 1961 counts (Anon, 1963*b*). Even so, difficulties remain, since there is evidence that some lampreys may spawn in the mouths of tributaries instead of upstream where the controls are applied (Wagner and Stauffer, 1962).

Here again an introduction of a species into a new environment through man's activities has upset the balance and is depriving man of food and livelihood. Biologists can only partially undo the damage, but the more we learn about every facet of the life of the species, the better are chances for its eventual suppression.

Rodent Control

One of the major groups of pests which man must contend with is the rodents. This group of mammals includes numerous species which eat cultivated plants, including their seeds and fruits (Fig. 11-2*a*, *b*), cause erosion problems by extensive burrowing, or dig unwanted and dangerous holes. Among the outstanding pest species of this group are the gophers, woodchucks, mice, rats, ground squirrels, and porcupines. Mice may cause severe damage by producing populations which bring about large losses to crops in a short time (see p. 309). Other species, such as the Norway rat, are more or less perennial and are a continual threat to the farmer's income, as well as being potential carriers of a variety of diseases. In some instances, however, it is difficult to evaluate a rodent, or some other species, as beneficial or detrimental. As Hamilton (1939) pointed out, animals such as pocket gophers, which undoubtedly do great harm to certain crops,

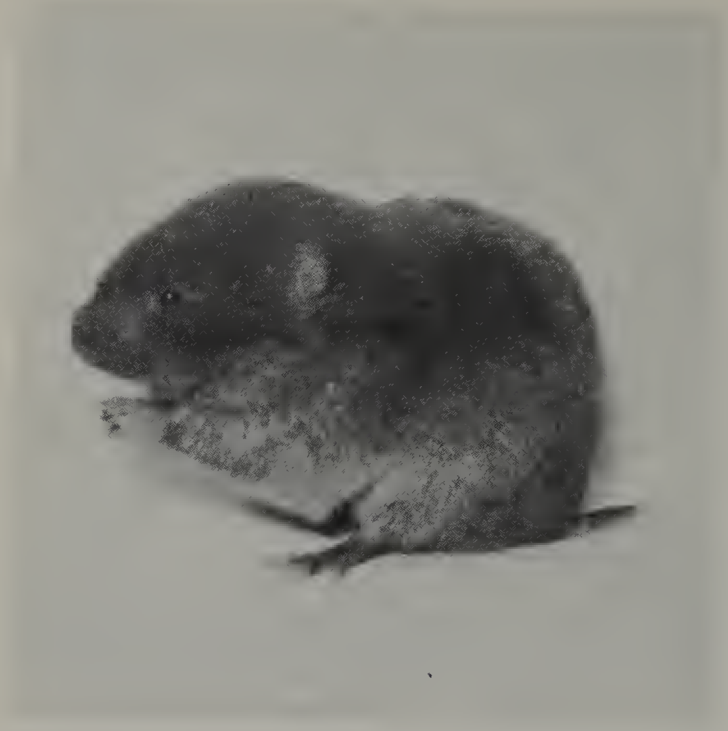

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Fig. 11-2*a* The pine mouse, *Pitymys pinetorum*, a destructive rodent of eastern North America.

may really be of great benefit through their part in the soil-building processes in watersheds where they are abundant. Knowledge of the full life history of any species is required before control measures should be applied.

Predator Control

Frequently certain animals are thought to present a threat to crops or to other wildlife, and there may be efforts to limit or lower the population of these unwanted species. Food analysis of the suspected species' diet over long periods of time may indicate that persecution of some of these animals is unjustified. By means of stomach-content analysis, scat examination, and careful observation of the species in the field, an accurate picture of the assets and liabilities of any animal species may be secured. Foxes are often thought of as raiders of chicken houses, but biologists recognize them as useful predators of field mice. They also eat fruits and insects, as well as rabbits and birds. Foxes, like so many other wildlife species, may be injurious at certain seasons or in certain localities but a benefit to man on other occasions and in other

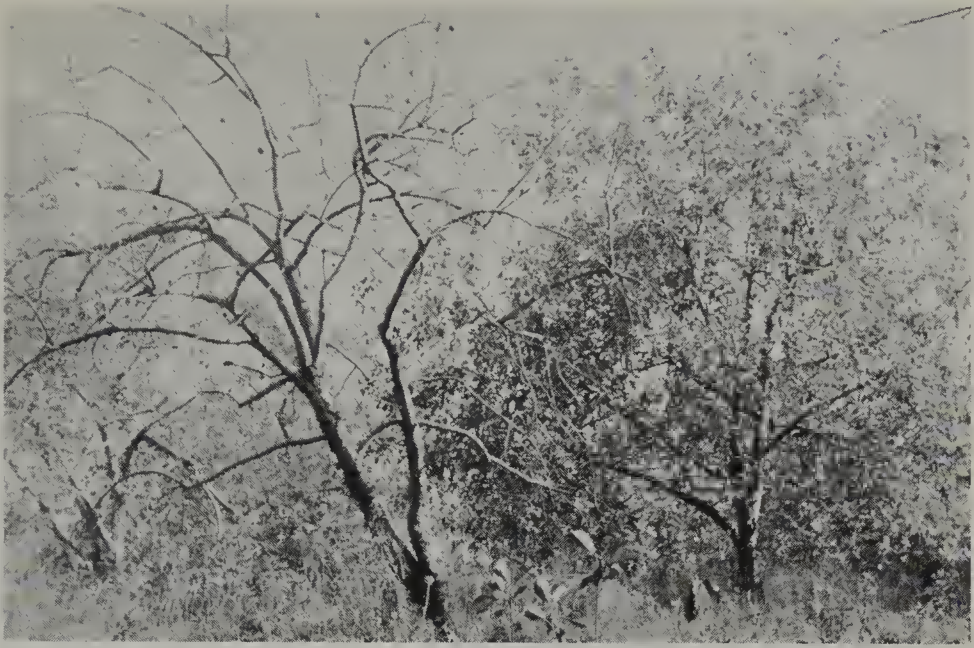

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Fig. 11-2*b* This apple tree was killed by the action of the pine mouse, which feeds on the bark and cambium layer of the roots and lower trunk.

places. This fact must not be forgotten in estimating the economic importance of any species.

Control of Disease-carrying Animals

Although most field biologists are not directly concerned with medicine, they may frequently contribute to the solution of medical problems when organisms which they have studied are involved in diseases. Frequently insects and their near relatives figure prominently in the health problems of the human race. Especially important in this connection are lice, fleas, flies, mosquitoes, and ticks. Entomologists and other biologists are able to help in the control of disease by passing on the results of their research to physicians and others who are more directly concerned with the diseases. Detailed knowledge of the habits and occurrence of a species may be used to control an organism which is found to be connected with disease.

Rats, together with their fleas, have played an important part in the medical history of the human race, especially in their relation to bubonic plague and murine typhus. Mammalogists are still studying the population characteristics and ecology of rats in an effort to develop better control over them.

Mammals other than rats may also be reservoirs of disease. Recent cases of bubonic plague in this country, for example, have been traced to ground squirrels and rabbits which were acting as hosts to the disease organism. Rocky Mountain spotted fever, carried by ticks, is another disease of man which may exist in wild mammal populations such as rabbits and mice, and tularemia is frequently transmitted to man from rabbits.

Mammalogists have also been called upon in the control of rabies, for many wild animals, including foxes, raccoons, skunks, and certain bats, are known carriers of this dreaded disease. In New York, for example, red foxes have been trapped extensively in an effort to stop a rabies outbreak. At first a strip of land 5 to 10 miles wide around an area of infection was trapped to prevent spread of the disease—but without success. Further research revealed that red foxes frequently range at least 50 miles. Consequently, the trapping strip was increased to 50 miles in width (Colson, 1955). These trapping procedures have reduced the incidence and have sharply retarded the spread of the disease (Linhart, 1960). It is apparent that suppression and possible eradication of many diseases must depend, at least in part, on knowledge gained by biologists working in the field.

CONSERVATION

Conservationists have studied the human population in various countries around the world in relation to water, soil, and wildlife use. Writers such as Vogt (1948) paint a gloomy picture of the present and future for the human race. Although there are solutions to the conservation problem, largely based on knowledge gained within the last half century, starvation on a world-wide scale is a real possibility. Since 1940, the world population increased by nearly one-third. At the present rate of growth, within one hundred years it would be multiplied sixfold (Davis, 1963). Severe overpopulation, destructive land practices, cultural problems, and ignorance or disregard of conservation practices may be a more pressing problem than disarmament.

The Soil

Study of past agricultural practices has revealed what happens to produce the unhappy state in which man now finds his natural resources. Rainfall varies widely from one region of the world to the other, as does steepness of terrain. Where rainfall is relatively high, forests are the climax type of vegetation. Trees protect the soil although such soil is usually thin. If the forests are removed, especially on steep slopes, erosion may quickly occur (Fig. 11-3). Then the topsoil will wash down the streams, ruining the fertility of the soil. All too frequently, forests have been destroyed to make agricultural lands on hilly terrain where the soil was not suited for crops at the outset. As erosion proceeds, the soil becomes too poor to support crops. Frequently the land is used for grazing after it will no longer grow satisfactory crops, and if it is overgrazed, the last remaining topsoil will disappear along with most of the surviving vegetation. In some regions of the world, the final indignity to the land is performed by goats, which destroy any shrubs, trees, or grass which may remain.

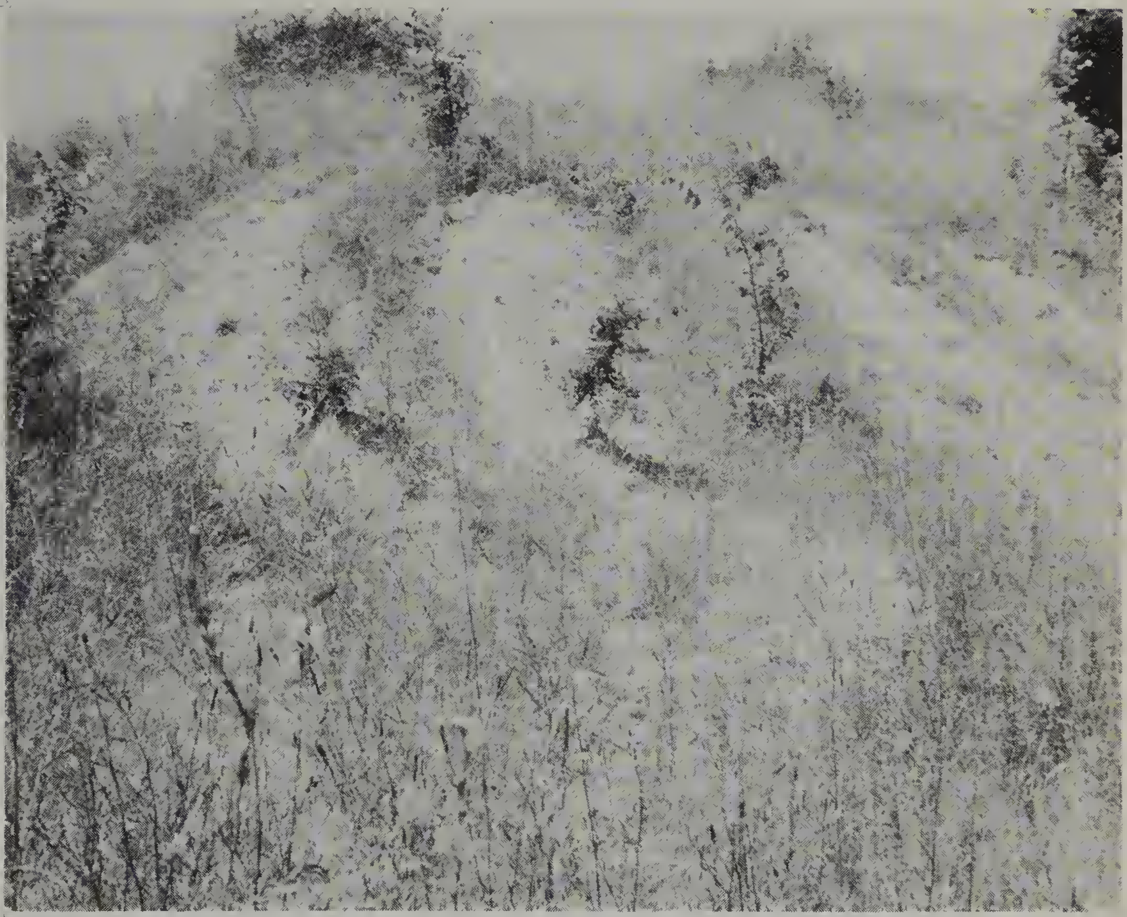

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Fig. 11-3 Sheet erosion on steep, hilly terrain.

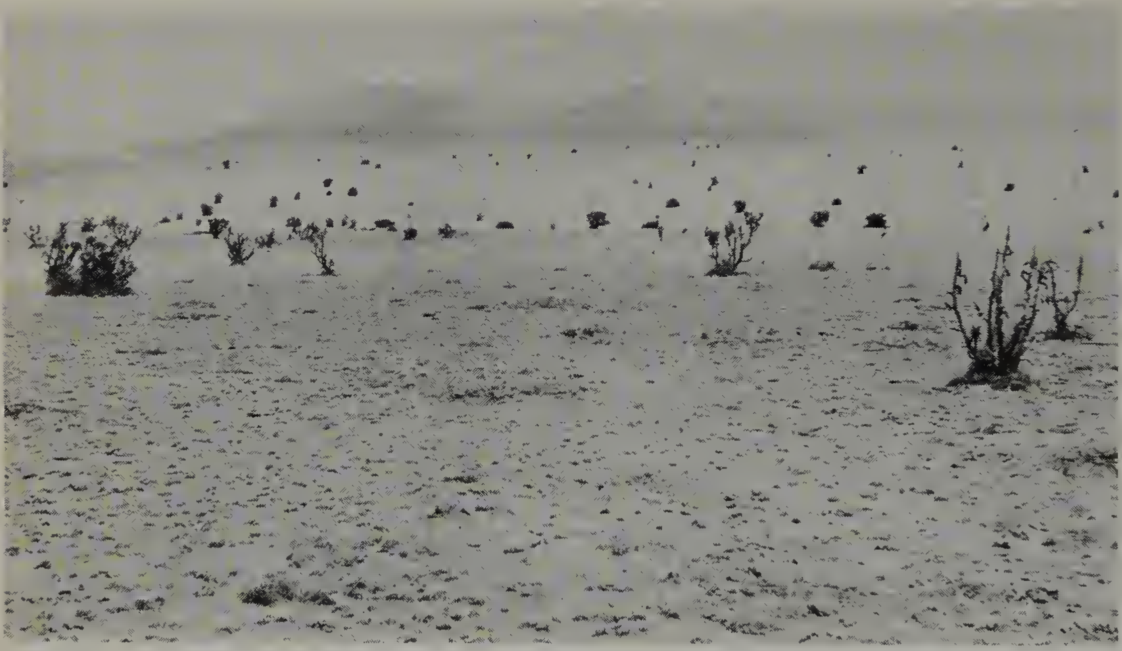

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Fig. 11-4 This overgrazed land has become desert because of poor agricultural practices.

The end result is a wasteland. This tragic situation may be seen today in Spain, Italy, Greece, and many other countries. In our own West, where rainfall is scanty but the terrain level, wind has been the damaging element, once man has allowed intensive farming, overgrazing, and other poor land practices to permit wind action. The result is the same as in the hilly forested regions—severe erosion and consequent loss of soil fertility.

Studies of succession (see Chaps. 6 and 7) indicate the length of time required to rebuild soil once accelerated erosion has occurred, and how such soil is made. From such studies, we discover that the natural climax community is a reliable indication of what type of farming a given region may support. The signs of overgrazing and some other poor land practices are also evidenced by the community type (Fig. 11-4).

Population Problems

The problem of the human population and its food supply comes within the concern of conservationists, for they are interested in the best possible use of all our resources. The studies of biologists involving wildlife may give some valuable clues to the causes and possible solutions of the human population problem. An animal such as the white-tailed deer serves as an example. Within recent years the population in various parts of the country has increased amazingly. In the eastern states the deer population was probably more or less stabilized before the coming of the white man. There were predators to prevent unduly high populations, and Indians hunted deer for food. With the invasion of the European, forests were cleared, and although predators were soon reduced or exterminated, hunting was intensive. As a result, the deer population declined. Unfortunately for man, many of the forest lands which were cleared for farms were soon eroded and then abandoned. The fields began to be restored to forest by means of succession, providing excellent food and cover for the deer. With this favorable condition, and without their natural predators, deer populations were able to grow even under considerable hunting pressure. Such pressure, of course, was stabilized by legislation, including buck laws and closed seasons. In recent years the deer have become a problem. In the agricultural regions of the Northeast, they have become so numerous as to become pests to the farmers. Their forest range is in many cases overgrazed. Now the problem has become one of reducing the overpopulation and overgrazing and the consequent mass starvation of deer in some areas. Hunters, disease, and lack of food are the population controls, since predators such as the wolves and cougars are gone from the area. If we compare this situation to the human one, we find that the natural controls over the human population are the same—disease, lack of food, and wars, which are another form of hunting. Increase in food through technical advances cannot continue indefinitely. As diseases are conquered, other means must become more important in limiting our population unless some new factor is introduced.

Is food the ultimate limiting factor in determining the maximum population of any species? As Elton (1947) indicated, although food supply must eventually establish the population limit, such a limit is seldom reached among herbivorous animals. Carnivores, however, are apparently frequently checked by lack of food. Under normal conditions, predators will act as a population check on herbivores, and when some disturbance, climatological or otherwise, allows a prey population to get ahead of its predators, parasites are usually the effective controls. If both of these fail, then starvation of a whole population may ensue. On the other hand, some biologists believe that natural populations may be limited chiefly by other means (see p. 308).

Errington (1963), who was one of the foremost students of predation in this country, was extremely skeptical of the idea that predators controlled their prey. He noted that organisms had mechanisms such as variable reproductive rates to compensate for population losses due to various agencies (predation, disease, weather, and so forth). Furthermore, when prey populations increase, predation on this population may increase, but other checks on the population also become more pronounced. Thus one cannot say that predation is *the* control of the prey population.

From knowledge gained in the study of many animal populations, we may arrive at the inescapable fact that something will eventually act to check the rise in human population. Vogt (1948) believes that the population is already being limited, mainly by starvation or poor nutrition, in many parts of the world. Undoubtedly other factors are also important in limiting the numbers of humans which the earth can support.

Without a doubt, the human population problem is one of the most serious and pressing which faces man's economy. In order that we may live at the highest standards of living possible under the circumstances, it is necessary to obtain the utmost use of all natural resources, including our forests, soil, water, minerals, and wildlife. Since there is only a certain amount of some of these resources such as oil, coal, iron, and other minerals, they must be conserved as much as possible. Unlike forests and game, they are not self-replenishing. Furthermore, as far as man's usage is concerned, soil is also in this category of nonreplenishable resources. Although new soil may be built by natural forces in a few thousand years, at the present rate of growth of the human population, man cannot wait that long. Poor soil, however, may be made into good soil in a few years under proper conservation practices. Our aim must be to reach a point at which the constructive processes of soil building are faster than the destructive forces of soil erosion.

Water

It is almost impossible to consider soil conservation without simultaneously considering water. The amount of rainfall in an area or, even more, the ratio between the amount of rainfall and the evaporation rate, largely determines the soil fertility by helping to determine the climax community and the amount of leaching. Where rain is abundant, as in the forest biome, and drainage is good, leaching is rapid, and thin soils result. In areas where there is moderate rainfall and less leaching, as in the prairie biome, the soils become deep and fertile.

By cutting forests or plowing grasslands and then planting crops, man often leaves the soil uncovered by vegetation for months at a time. Under such circumstances, erosion may occur at an incredible rate. Gustafson et al. (1949) tell of instances in colonial times in which land was made useless in 20 years because of poor care and subsequent erosion. Some of our richest prairie lands are also being eroded, although not so seriously as the grasslands of the Great Plains. These once-rich areas have become known as the Dust Bowl in recent years because of the severe wind erosion which has occurred there (Fig. 11-5*a*, *b*). Yet it is estimated that the muddy Missisippi, which drains the prairie region, deposits as much as 400 million tons of rich prairie soil in the Gulf of Mexico each year (Bennett, 1936).

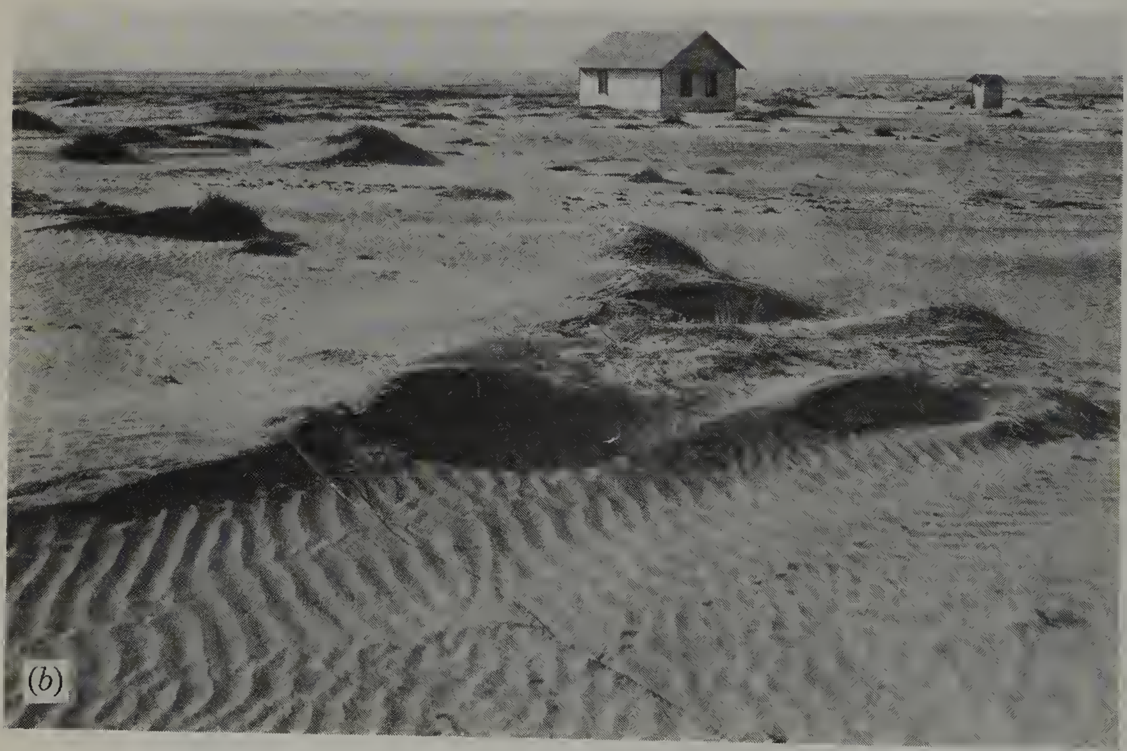
One effect of plowing is to make a region drier through the increased evaporation rate (Gustafson et al., 1949). In the prairie region of Illinois, the first farmers settled along the streams in the wooded region to make their farms. There were probably several reasons for this: the availability of water, the idea that soil which supports a forest must be more fertile than soil which grows only prairie grasses, and the need for timber for buildings. Furthermore, frequent grass fires made the prairies dangerous. In addition, at that time the prairie soils were frequently so wet that they could not be turned with the plows then available. Aged residents of this region still recall the marshy areas where grass grew as high as the shoulder of a man on horseback. These lands, now largely planted to corn, soybeans, and wheat, are far from wet today.

Erosion-control Methods

Soil conservationists are attempting to do something about the alarming situation resulting from soil erosion. They study the cause of soil erosion and then look for practical ways to prevent it. The fundamental clue to much of the problem

Soil Conservation Service, U.S.D.A.

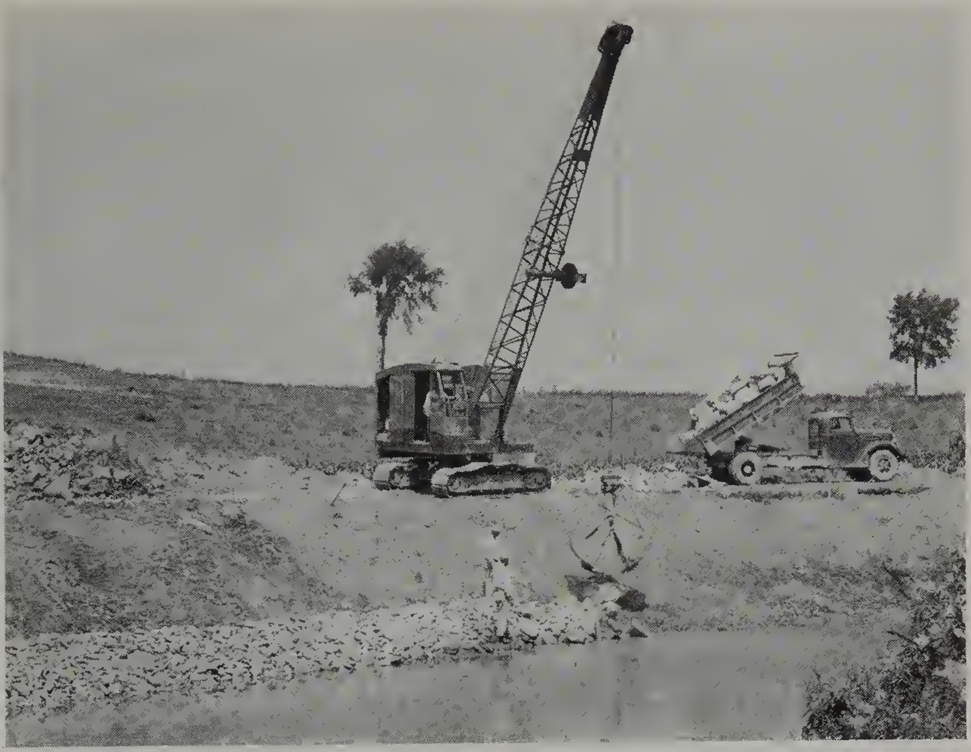
(*a*) An approaching dust storm.



Soil Conservation Service, U.S.D.A.

(*b*) Effect of severe wind erosion in Texas. The land has been abandoned after successive crop failures.

Fig. 11-5 Wind erosion in the Dust Bowl.



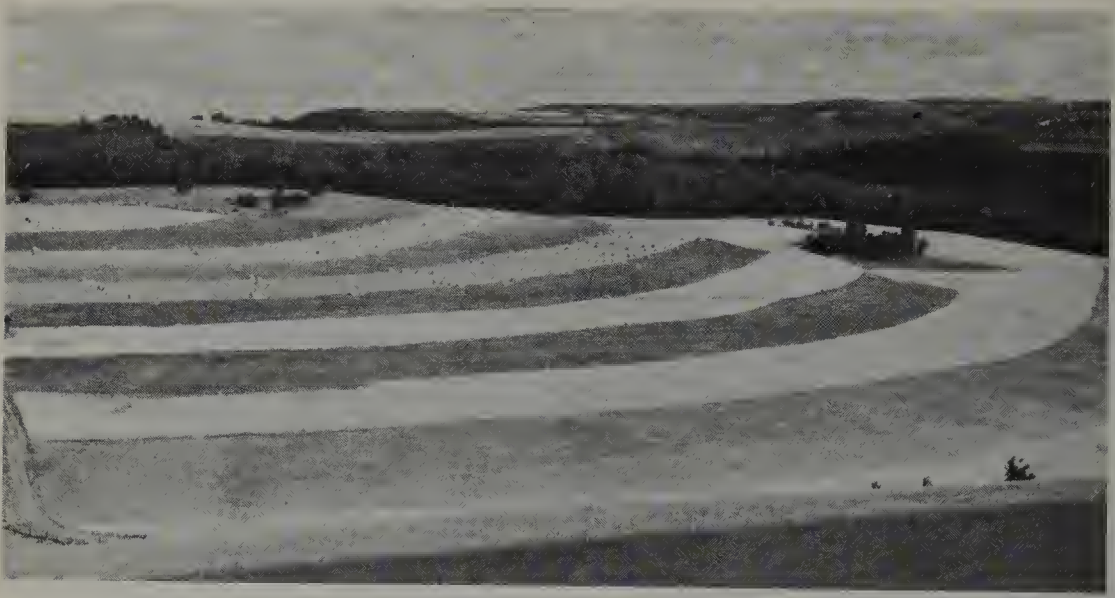
Soil Conservation Service, U.S.D.A.

Fig. 11-6 Stream-bank improvement. Stones slow down bank erosion.

of soil conservation is in proper use of the land. Certain lands should never be put to agricultural use, for either crops or grazing. They are too hilly and the soil is too thin. Other lands should be used only with the utmost care, including all the preventive measures known against soil erosion. Crop rotation may reduce the drain of fertility from the soil. Stream-bank improvement (Fig. 11-6) prevents the erosion of land along waterways. Contour-strip cropping permits the use of relatively hilly land without undue erosion (Fig. 11-7). Even the best croplands on level soil must be used with caution, according to wise conservation practices, if the soil is to be maintained.

Flood Control

Another major factor in control of erosion is the subject of heated controversy. In most parts of the country, water is the main erosive force. Erosion control, then, must involve watershed protection and stream control. If water flows from the hills and valleys too rapidly, soil is eroded and the subsurface soils do not benefit from the rain. Moreover, as a



Soil Conservation Service, U.S.D.A.

Fig. 11-7 Contour strip cropping on sloping ground prevents rapid erosion and conserves soil.

result of this rapid excursion of water from the watersheds, floods occur in the rainy season, and droughts at other times.

The United States Army Corps of Engineers and the Bureau of Reclamation have been trying to remedy the major flood threats by building dams on the larger waterways where floods have occurred. The water impounded by these huge dams is used for hydroelectric power, irrigation, and recreation, in addition to controlling the floodwaters rushing down the rivers (Fig. 11-8). Many conservationists object to this method of flood control and challenge its soundness as an erosion-control device. They believe that the wisest and most economically sound answer to the problem is to protect the watershed, thus preventing soil erosion as well as floods. They point out that if the soil does not erode, the organic matter of the soil will remain and will help the soil to absorb and hold the precipitation. Without this kind of control, big dams are not economically sound, they feel, because the eroded soil will be carried into the reservoirs behind the dams, which will quickly fill with silt and be rendered useless. Hoover Dam, for example, was completed in 1936, and by 1948 over 75 feet of sediment had accumulated on the bottom near the dam, and much more upstream (Gould, 1954). There has also been

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Fig. 11-8 Large dams such as the Hoover Dam shown here are used for hydroelectric power, irrigation, and recreation, as well as for flood control.

objection to some large dams because they have obstructed the passage of fishes to their spawning grounds. In some cases, notably in the Northwest, this situation has been alleviated by specially constructed fish ladders which bypass the dams.

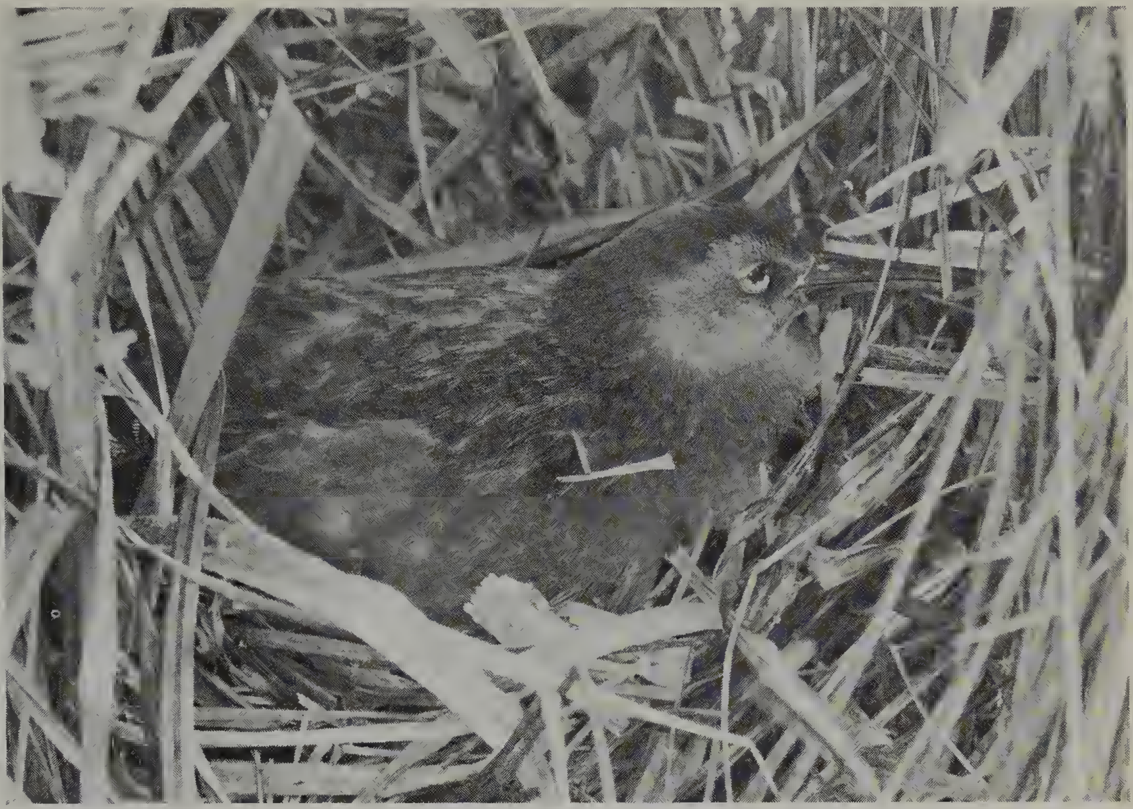
Many conservationists favor dams on the smaller streams in addition to watershed control. However, such dams might be of little value for hydroelectric power. Again, conservationists point out that it is difficult or impossible to have one dam effectively serve as many purposes as the proponents of large dams claim. For example, in the springtime dams should be empty for effective flood control when the high water sweeps down the stream; but they must be full if they are to be used for irrigation. If, during the summer, the water is used for irrigation, the level will be lowered, decreasing the value of the structure for recreation and power. However, on some streams dams may be usable for several purposes because the flood season is predictable and of relatively short duration. On other streams, dams may be used only for flood control because floods may occur at any time of the year. A further objection to large dams is that much land, often fertile and valuable, is inundated by their creation. Actually, both dams and soil-conservation practices are needed to solve our soil- and water-conservation problems. If soil-conservation practices are not followed, dams silt up rapidly. On the other hand, soil-conservation practices alone cannot prevent all types of floods or provide large amounts of water for hydroelectric power and other uses.

Drainage of Wetlands

Another conflict of interests comes between conservationists and the Bureau of Reclamation in the efforts to drain swampy or marshy areas. The purpose of such drainage, carried on by the Reclamation Bureau, is to increase the amount of land available for agriculture. Conservationists object to further draining of wetlands for several reasons. Proponents of watershed control point out that swamps and marshes are natural reservoirs which are helpful in preventing excessive runoff of precipitation. Biologists insist that marshy areas are of great value because they are the refuge of waterfowl and many other important kinds of wildlife. In fact, most conservationists would like to see much of the formerly reclaimed land returned to marsh habitat and further draining stopped.

If marshes continue to be destroyed, waterfowl must decline, for only in the wetlands will they live and reproduce (Fig. 11-9). At present, the area of habitats suitable for wildfowl is being reduced steadily. In some areas, such as on the Pacific coast, so much marshland has been drained for agricultural purposes that migrant waterfowl have become pests, destroying the crops in the regions that were once their natural feeding grounds. Farmers attempting to protect their crops add to the heavy hunting pressure from sportsmen, and this may prove to be disastrous to the bird populations if suitable habitat is not provided.

Another argument against drainage of wetlands is that such action often proves to be fruitless or more costly than the results justify. Frequently land that is drained is found to be useless for agricultural purposes due to the chemical nature



E. G. Tabor

Fig. 11-9 Wetlands provide nesting sites for many species of waterfowl, rails, and other birds. Here a Virginia rail is incubating eggs in a marsh.

of the soil. Furthermore, it has been discovered that drainage of such areas may result in lowering the water table of surrounding land, making it less productive. In view of these serious disadvantages of wetland drainage, it would seem logical to make a study to assay the value of the wetland in terms of wildlife and water resources, and then compare this to the probable value of the land for agriculture and the costs involved in producing and sustaining the drainage.

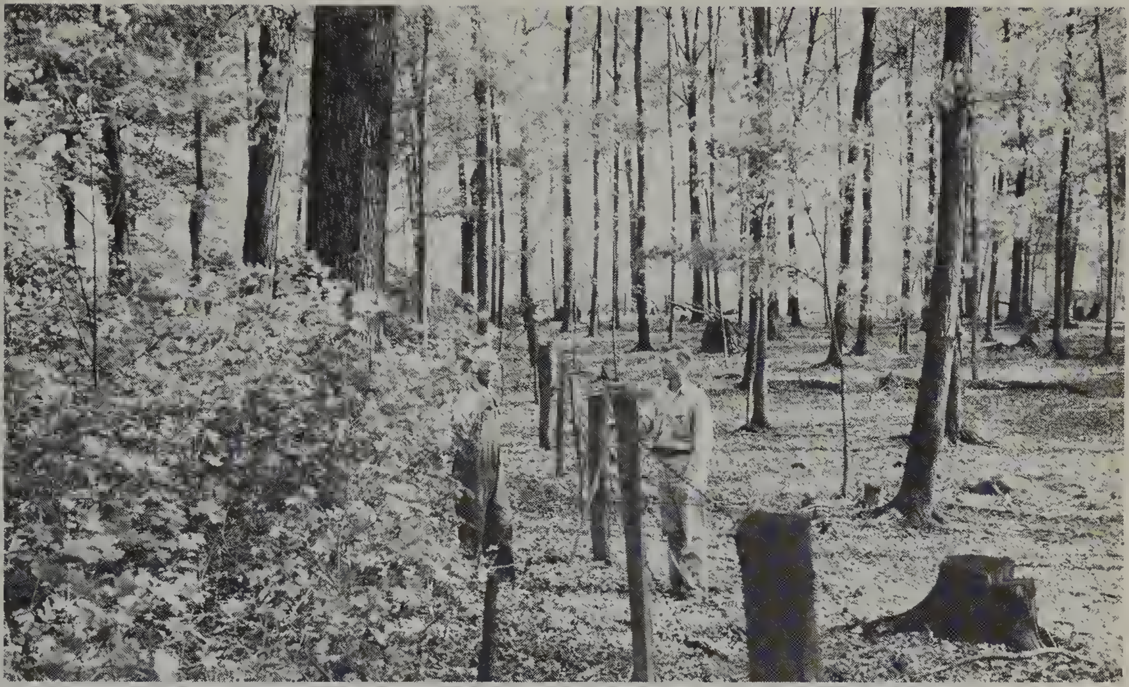
Pollution Control

A final major phase of water conservation is the problem of pollution. Many cities and industrial plants continue to dump wastes into streams. Not only does this practice make the use of such water for human consumption impossible without costly processing, but it also creates health hazards and damages aquatic organisms. The putrefaction of sewage by bacteria consumes oxygen and consequently affects organisms such as fish, which require large amounts of oxygen. Toxic wastes in the rivers may also kill fish and other food animals, such as mollusks. Even if one does not care about the effects of industrial wastes, human sewage, and residues of agricultural pesticides on aquatic organisms, everyone should be concerned with the condition of the water he drinks. For a readable account of the many problems involved in abatement of pollution of drinking water, see Tarzwell (1963).

On the eastern seaboard, the shad industry offers a good example of the damages which pollution may cause. The population of shad, a highly desirable food fish, has shown wide fluctuations recently. In good years, the catch might reach 4 million pounds, while in poor years it might fall to 40 thousand pounds (Talbot, 1954). This species is anadromous, spawning in certain large rivers along the coast from Florida to Canada. A number of studies by the U.S. Fish and Wildlife Service and the conservation departments of New York and New Jersey showed that pollution was one of the major factors involved in the decline of this species. Sewage and other wastes from New York City and other cities along the Hudson River have caused the last 150 miles of the river to be seriously polluted. It is believed that pollution control in this area would result in a great increase in the shad population of the river. Pollution creates similar problems in most of our major rivers and in many smaller streams, often because money will not be expended to process wastes properly. In some instances, however, there is no known way to process wastes so that they will not be harmful.

Forest Conservation

Our forest lands are not in an exemplary condition either, although they may be restored; so the chances for their improvement are greater than with soil. Of 1,072 million acres originally in forest, only 624 million remain forested, and of this only 45 million acres are in a condition similar to the virgin state (Buell, 1949). Not only are our forests economically important in themselves and hence deserving of the studies of biologists, but the welfare of our forests is intimately connected with that of the soil, water, and wildlife. Forestry management is practiced mainly on government-owned lands and on larger privately owned forests. It is of course aimed at the best and fullest possible use of our forests and at sustained yield over an indefinite period of time. In addition to proper cutting, foresters are concerned with control of pests



Soil Conservation Service, U.S.D.A.

Fig. 11-10 Ten years of protection from grazing has allowed recovery of the wood lot on the left. On the right, grazing has destroyed saplings and leaf litter, allowing erosion and compaction of the soil.

and fire, protection of watersheds, proper use of land by large game and cattle, and successional problems (Fig. 11-10).

Forest Fire. Protection from fires is one of the major problems of foresters. Forest fires annually consume appalling amounts of our forests (Fig. 11-11). In 1947, for example, fires burned more than 23,226,000 acres of forest, doing 55 million dollars' worth of damage (Brown, 1949). The loss of timber in itself is serious enough, but fires also mean destruction of the litter on the soil and consequent loss of protection of the topsoil from erosion. The loss of wildlife in large fires may also be great. After a fire, growth of a forest back to the condition where it will produce timber useful to man may take at least a century.

The most effective way to reduce fire losses is, obviously, prevention of forest fires. Nine out of ten wildfires are caused by man, seven out of ten through carelessness. Education of the public in the matters of how to safeguard against careless use of fires in forests and effective enforcement of regulations is, therefore, a first step in fire prevention. Foresters maintain lookouts and use aerial reconnaissance to spot blazes.

N.Y. State Conservation Dept.

Fig. 11-11 Even in the well-populated northeastern states, forest fires cause immense losses.

Mechanization of forest-fire-fighting equipment has greatly increased man's ability to cope with the problem. Bulldozers are able to clear fire lanes, flame throwers are used to start backfires, and roads and trucks aid greatly in gaining rapid access to burning areas. Development of aerial fire-fighting techniques has proved a great success, especially in wilder parts of our country. Aerial photographs of fires give a better idea of the situation in a shorter time than was previously possible. Formerly, a blaze which started in a mountainous region was difficult to reach, so that by the time fire-fighters arrived, the blaze might already be large. Now highly trained men and fire-fighting equipment are parachuted in to control flames quickly.

Forest Insects. Another cause of loss to our forests is insect damage. It is estimated that insects cause as much damage to forests as fire (Haeussler, 1952). Some of these insects, being introduced species, are like the Japanese beetle living in new territory without their normal predators and parasites. Included in this category are the European elm bark beetle and the gypsy moth. Others, like the Engelmann spruce beetle, the spruce budworm, and the tussock moth, are native. Native species may reach epidemic proportions as a result of natural catastrophes in the forest. For example the Engelmann spruce beetle, which destroyed a large proportion of the spruce in national parks in Colorado from 1942 to 1947, probably was able to build up its population on weakened trees blown over by a severe windstorm in 1939 (Wygant and Nelson, 1949).

Whether they are introduced or native, the forest insect pests present a difficult problem of control to the forester. Especially in the western United States, it is frequently difficult to detect pest outbreaks until they have already done great damage. This is in part because of the difficulty that rough terrain imposes in making forest insect surveys. Rough terrain also hampers effective treatment and survey of the results of the treatment.

Again, each insect may possess special characteristics that make its control different from that of other species. An insect may harm trees in a variety of ways—from defoliation, which weakens the tree, to destruction of fruit or seeds, which prevents reproduction. Chemical treatments have been developed for the control of outbreaks of defoliating types of forest insects by means of aerial spraying (Craighead and Miller, 1949). In the Northeast the gypsy moth, which defoliates deciduous trees, is now largely controlled by aerial spraying of DDT. Although quarantine and intensive control measures have been used against this imported pest, the moth has spread further into the Middle Atlantic states from New England, especially since 1953. The spread of the population is easily noted with gypsy moth traps which attract males within a radius of one-half mile by means of bait manufactured from the female sex glands (Masterson and Mitchell, 1956).

For many of the other insects which damage forests, biological control may prove to be the answer, but this requires a detailed study of the ecology of each species under consideration. Unfortunately, there is as yet no known method of control for many of our most serious forest insect pests, other than aerial spraying with nonspecific pesticides.

Watersheds. The importance of forest fires and insect pests is frequently felt in watershed control, for destruction of the forests by fires and pests may cause serious erosion. Forests on the lands that catch the water which eventually supplies crops and cities have several protective actions. They prevent rain from hitting the soil directly and thus eroding it. The roots of the trees help to hold the soil and make it porous, so that the water will soak into the ground and travel to streams by way of the water table, instead of running off along the surface to cause floods. The litter from the trees covers the ground and prevents it from drying rapidly. Eventually, this litter becomes part of the soil, maintaining its fertility and increasing its water-holding capacity. If the forests are destroyed by fire or insects, periods of high precipitation will cause washing away of the leaf litter, along with some of the soil. The colloidal soil suspended in this water clogs up the pores of the soil in the ground so that less water can soak in, compounding the difficulty. Since water cannot soak into the ground, runoff is increased and erosion proceeds at a still faster rate. The results are floods during times of high precipitation or melting of snow, and lowering of the water table so that streams dry up in summer.

In the West, however, water is scarce because of the low rainfall. People in this area argue that trees lose a great deal of water to the atmosphere from their leaves (transpiration) above and beyond the amount that would be evaporated from the soil without the shade of trees. Farmers therefore asked for the cutting of the watershed forests so that more water would be available to them for agriculture in the valleys. Wilm (1949) described several long-term experiments that were conducted to determine the results that cutting of timber on watersheds would have on the production of water and on erosion. These experiments showed that under certain watershed conditions selective cutting of the mature trees did increase the flow of water in streams substantially, and that consequent erosion was only slight. Cutting could not be carried out on all watersheds with this beneficial effect, however, and in any case care had to be taken to avoid erosion.

Of course, some parts of watersheds are planted in crops, and here the usual practices of soil conservation must be used in addition to small dams and basins to collect debris that is washed down during floods. Various stream-improvement devices are also used to prevent erosion of stream banks. As Phillips and Frank (1949) pointed out, watershed control alone will not prevent floods. Reservoirs and dams are also required in an integrated program with watershed treatments.

Forest Management

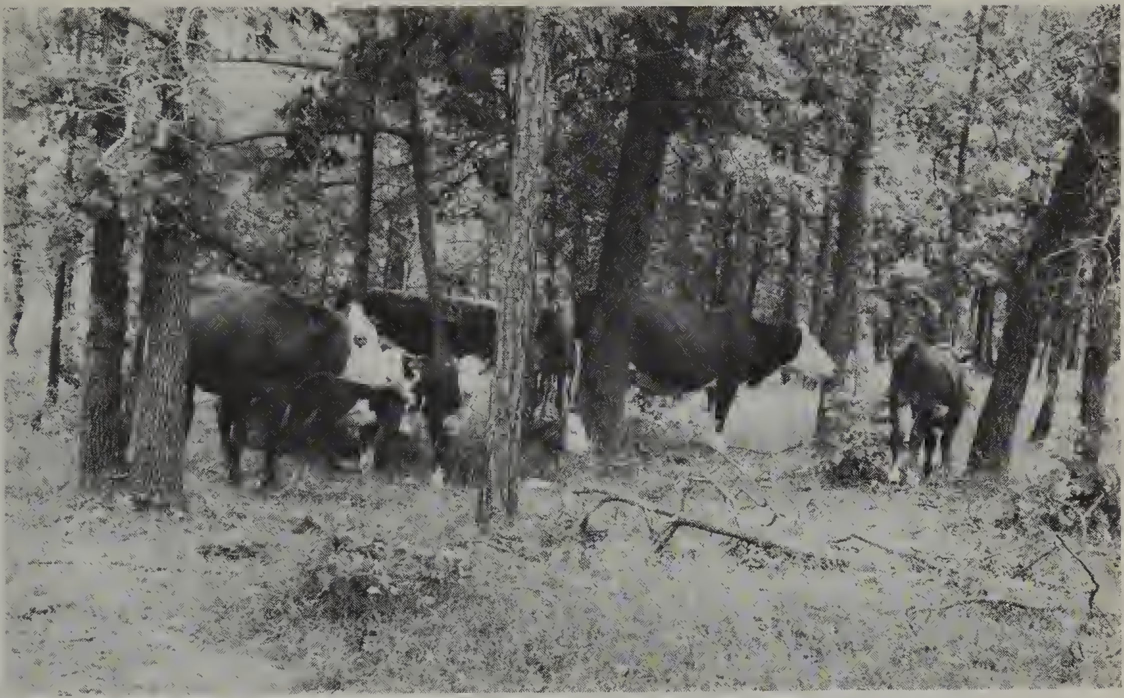
The way in which forests are used is the concern of forest managers. They are interested in forest production, including maximum sustained yield of timber, reforestation, grazing, and forest succession. From long-continued studies, methods of cutting have been developed so that forests may be cut for best advantage of the present and future yields. The method of colonial times was to cut down a forest completely, which frequently led to erosion and loss of productivity.

Several methods of cutting now employed are based on ecological principles, especially on the concept of succession. Thus, in forests composed of dominants whose seedlings are tolerant of shade, such as beech and sugar maple, only the mature, diseased, or overcrowded trees are removed. This *selective cutting* system allows a continual natural reforestation and an almost continual yield. Such a forest would have trees of nearly all ages. Some types of trees do not flourish under these conditions, and so other methods of cutting must be used. Harvest of such species may be accomplished by cutting all of the mature trees at once without detrimental effects. One such method, known as the *shelterwood* system, employs two or more cuttings during the growth of a stand of trees and a cutting of all the mature trees in the final harvest. The earlier cuttings allow seedlings to become established so that when the mature trees are finally harvested, reforestation is already under way. Another method of cutting is a modified *clear-cutting* system. Small irregular strips or sections are cut down entirely, but they are small enough so that seeds from the surrounding mature trees will reforest the clearings. As long as the clearings are far enough apart, erosion is not a serious problem. Such a cutting system is particularly good for those species of trees whose seedlings require or tolerate large amounts of sunlight.

Succession figures prominently in cutting systems and reforestation. Thus sugar maple seedlings require only 2 per cent sunlight, while seedlings of loblolly pine need the full benefits of sunlight (Barrett, 1949). In other words, seedlings of loblolly pine will not grow in the shade of older trees. They are not part of the climax community but are found at an earlier stage of succession before deep shade has developed. Sugar maple, on the other hand, forms a large part of the climax forest, and seedlings of this species normally grow under the deep shade of the mature trees. If trees which occur in early successional stages are not desired as timber trees, the forests should therefore not be clear-cut. This is true in the Northeast, where clear-cutting results in a second growth of inferior species such as gray birch, poplar, and red maple under most conditions. If species of the early stages of succession are desirable trees and are preferred to species of the climax, one of the clear-cutting methods should be used.

Reforestation. A knowledge of succession can also be used to hasten reforestation by indicating what kinds of trees can be planted successfully under given circumstances. It would be useless to plant hard maple seedlings, for example, in an open field. Artificial reforestation is accomplished either by growing seedlings in the nursery or by direct seeding. The former method is more costly, but avoids some difficulties which are caused by direct seeding, namely, losses of seeds due to action of rodents, birds, insects, and the weather. The fact that small mammals can affect reforestation and the direction of succession is demonstrated in the studies of Tevis (1956). He described a situation in a Douglas fir forest of California in which several rodents, including white-footed mice, chickarees (red squirrels), and Townsend chipmunks destroy a large percentage of the seeds of the Douglas fir in clear-cut areas. The result is that Douglas fir is at a disadvantage in succession, and instead of a climax community with this desirable species as dominant, we find that the undesirable tan oak becomes established. In the absence of Douglas fir, the mice are able to thrive on the cut-over areas by eating the numerous insects which feed on the saplings of the oaks and other vegetation associated with the various successional stages. Whenever Douglas fir seeds are available, however, they will eat them avidly.

Grazing in Forests. Grazing is often practiced on forest lands, especially in the more open forests of the West. Grassy areas in the forested regions provide food for livestock and are important in the local economy, but overgrazing and browsing can be detrimental to the forests. Young seedlings may be eaten, and the conditions for erosion may be established. Cattle will trample down the soil when it is wet, making it hard when it dries. The litter may be destroyed, allowing abnormal drying during the warm months. Both of these conditions foster rapid runoff of precipitation by preventing the soil from



Soil Conservation Service, U.S.D.A.

Fig. 11-12 Forest grazing is holding back reproduction of these pines in a southeastern forest and is also forcing out the grass.

soaking up rain water, and this leads to accelerated erosion (Fig. 11-12; see also Fig. 11-10).

Wildlife Conservation

The value of wildlife is rather difficult to appraise, for it must include other factors besides the actual monetary value of the animals as food. The aesthetic value of wildlife, in terms of human enjoyment, cannot readily be measured in dollars and cents. The recreational value of hunting and fishing, as well as bird watching and related pursuits, is likewise unmeasurable. Easier to determine, and very important to the locality where the game lives, is the expenditure of money in the area for food, ammunition, guns, camping equipment, and other supplies to the tune of millions of dollars per year. In any case, wildlife is of great economic worth and is sufficiently important to warrant the time and money spent by biologists in their efforts to learn about its natural history, conservation, and management.

Wildlife management is that phase of biology which is concerned with the best possible development, use, and conservation of wildlife. Most of the species involved are not considered commercially important, although such economically important species as the oyster, the lake trout, and the various fur bearers are studied. The significance of most of the species, however, is due to their aesthetic and recreational value. The object of management for all species is to make sure that a species does not become extinct because of overexploitation, disease, or the various natural causes which may threaten. On the other hand, wildlife management is also aimed at full utilization of all our wildlife for the benefit of the greatest possible number of people.

Although the idea of management of wildlife sounds like a simple one, it is frequently difficult to carry out. Conflicts arise over the use of land by wildlife, as opposed to agriculture, and jurisdictional problems due to land ownership or control often occur. Most pressing is the need for information on the life history of the many species concerned. In the report "The Nation Looks at Its Resources" (1953), enlightening discussions by the men most interested in wildlife management point out several areas in which controversy over land use creates still unsolved problems. The major ones concern the competition of deer and cattle for grazing lands in the western forests; the use of wetlands for waterfowl or their drainage for crops; and the problem of managing forests for the multiple uses of their timber, grazing, wildlife, and water conservation.

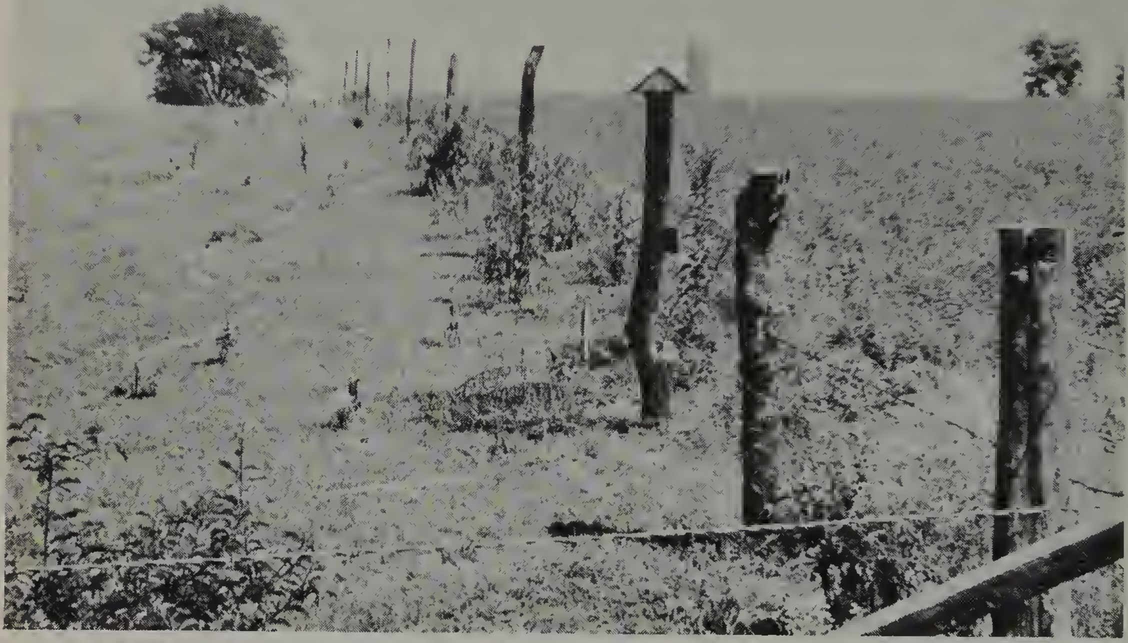
Jurisdictional problems over wildlife management may occur, as in forest management, between different government agencies, since intelligent management may require large areas, regardless of artificial political boundaries. In areas where most of the land is broken up into small, privately owned plots, uncooperative landowners can make proper management impossible. Deer herds, for example, may utilize lands of several owners. If one or more of these owners prevent hunting on their land, they may thus form a refuge for the herd during the hunting season. Without the necessary harvesting of the surplus, the herd may grow to a level which endangers crops on the lands of surrounding owners. Thus wildlife management is not entirely a matter of biology, although in the final analysis it must depend on fundamental biological knowledge of the species.

Data Needed for Wildlife Management. Information that especially aids management may be grouped into six main categories: habitat requirements, food habits, reproduction, population size and fluctuations, range, and interrelationships with other species. If this seems to cover almost the total ecology of the species, it is probably a correct impression. However, certain facets of the natural history of a species may be of more importance than others in its management.

When a species is to be managed, one of the first things that must be known is the size of the population (see p. 303). Population censuses are taken to discover the local or over-all abundance of a species, whether or not the population fluctuates widely, and if so, what the causes may be for the fluctuations. The accumulation of this knowledge may elude the investigator, even after a full ecological investigation; yet it must be attempted. The problems of population study are considered in detail in Chap. 9.

One of the major factors to consider in searching for methods of management of a population is its interrelationships with other species. Such interrelationships may be helpful or harmful. Predators, parasites, and disease organisms tend to diminish the population. Frequently the activities of man may be the cause of the decline of a species and of the resultant necessity for management. The Alaska fur seal is a good example. Commercial hunting pressure by American, Russian, and Japanese sealers had reduced this species drastically prior to 1910, threatening to exterminate it. There was no question that man was the factor which created these population difficulties. By treaty among the nations most concerned with this industry, strict protection was accorded to the seal population, and the species began to recuperate. As the seals became more abundant, some harvesting was again possible. But this time it was carefully controlled and based on complete studies of reproduction, natural mortality, and the other factors which affect the welfare of the species. If the same danger of extermination were to be prevented from occurring again, much had to be known about the ecology of the species. First the population as a whole had to be censused each year to determine the rate of population increase. Details of reproduction, such as time and age of breeding, gestation period, number of young per litter, conditions suitable for breeding, and sex ratios most suitable for maximum production had to be determined.

After such studies had begun (see Bartholomew and Hoel, 1953), a hunting season and maximum number of animals that might be taken annually could be established without jeopardizing the existence of the species. In 1956, the



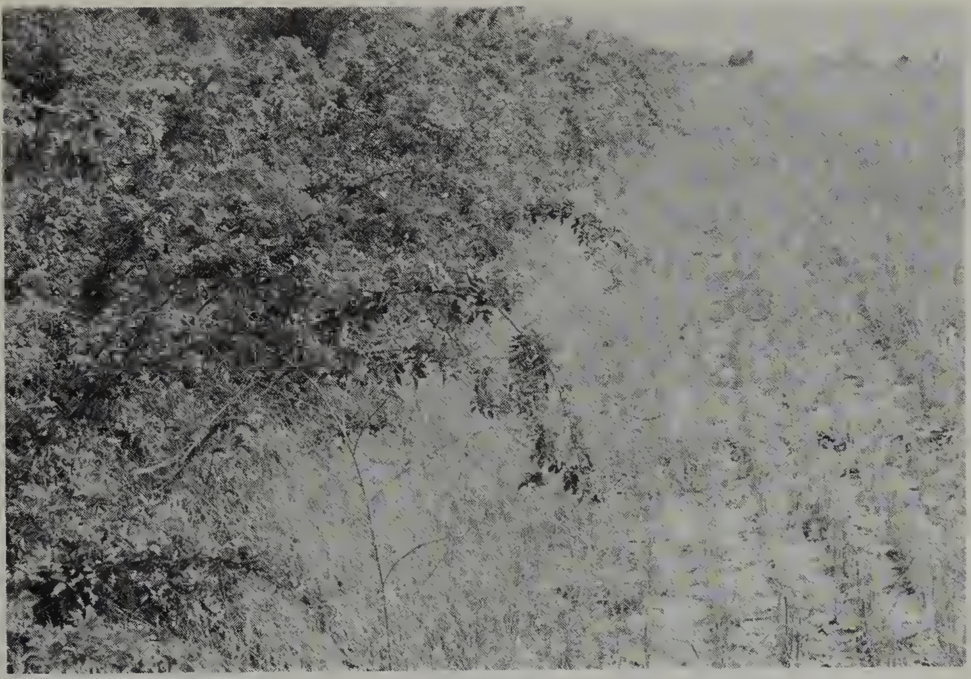
William E. Werner, Jr.

Fig. 11-13 Clean fencerows provide no cover for wildlife which might benefit the farmer.

first large harvest (4,641) of female seals was made, and in 1957, a still larger number (8,614) was taken. From examination of these specimens, more was learned of the reproductive potential of the species (Abegglen and Roppel, 1959).

The Food and Cover Problems. Sometimes man is not the direct cause of the decrease of a species, but he may affect its natural survival, causing a management problem. In agricultural lands there has been a tendency to clear land up to the fence (Fig. 11-13). Such a practice leaves very little natural food and cover for rabbits and important game species. The young or adults then become the easy prey of various predators. By leaving brush along the fence, cover is available within easy reach of their feeding area (Fig. 11-14). Predators thereby have a more difficult time catching the rabbits, and the population is allowed to maintain itself at a higher level (Fig. 11-15).

With many of our game species, food may limit their numbers at certain times. The problem of game management

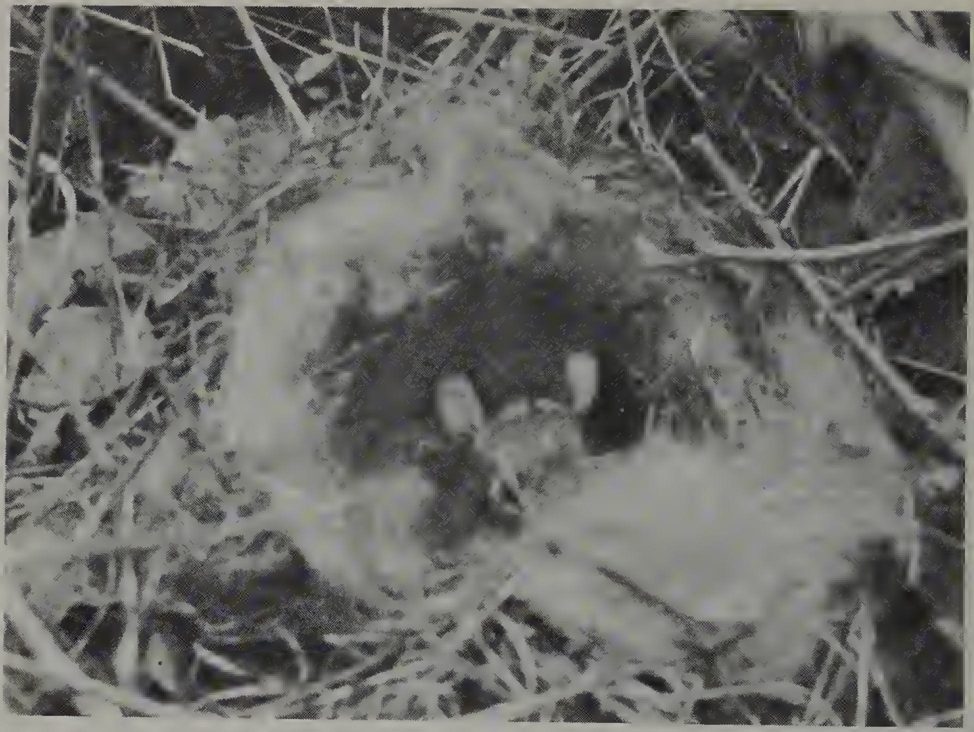


William E. Werner, Jr.

Fig. 11-14 A multiflora rose hedge provides effective control of livestock and also furnishes food and cover for wildlife.

is then to find ways of supplementing the food supply, especially in unfavorable seasons. Grouse, for example, may be aided by the introduction of certain kinds of apple trees in parts of their range where winter food may be scarce. Waterfowl are substantially aided by water-control measures, for example, by small dams or dikes. Such measures provide a more stable environment, including the food and water supply during the dry summer months. The planting of natural foods such as wild rice near their feeding areas is also used to aid waterfowl. In some cases, as in the regions of California previously mentioned, suitable waterfowl habitat has been so reduced that these birds have been specially fed by hand and on grain and grass crops grown in refuges, in order to reduce their damage to agricultural crops (Biehn, 1951).

Competition for food between wildlife species often assumes importance in management. This is especially true in the management of fish populations. Some of the pan fish, such as sunfish and perch, are competitors for the same food as the larger and more desired game fish, such as pickerel and bass. If the pan fish increase in numbers, they eat up not only the supply of food for the game fish but also that needed



Allen H. Benton

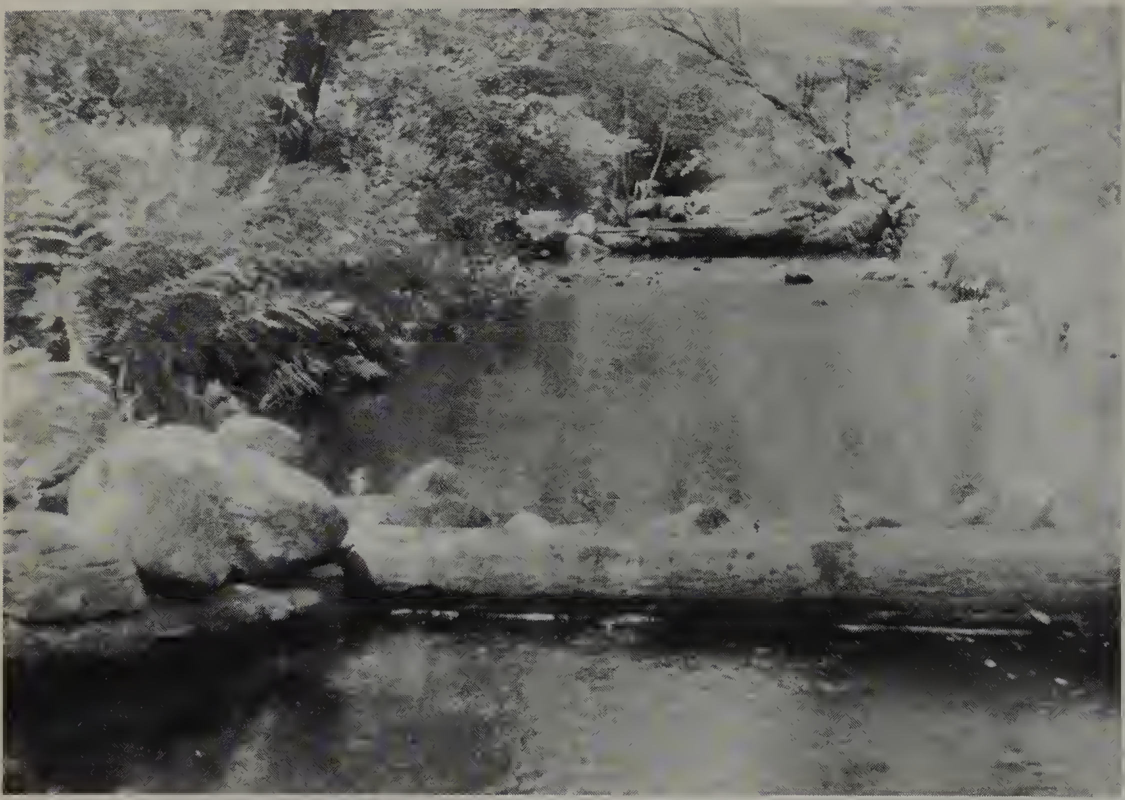
Fig. 11-15 A rabbit nest (opened to show the young inside) in a brush pile along a hedgerow.

by other members of their own species. One consequence is that the pan fish are stunted and hence become even less desirable. More fishing pressure may then be placed upon the game fish. This in turn reduces the population of the larger species. The end result is a large amount of small pan fish and very few game fish. Control of such a situation is not easy, but reduction of the pan fish may be accomplished by induced fishing pressure on them or by selective netting. In some lakes and ponds the drastic step of killing all the fish and restocking may be necessary (Petty, 1953). These problems of fish production are especially common in farm ponds. For an extensive discussion of the management of such impoundments, see Dendy (1963).

The Predator Problem. The opposite situation, overabundance of undesirable predators, produces a different and exceedingly complex problem for wildlife managers. As is so often the case in biology, there is no one solution that will apply to all situations. In fact, it seems that biologists cannot agree on whether predator control is always suitable, let alone how to accomplish it. Latham (1951) summarized the various present views on this controversial issue. He pointed out that people who think of the losses of individual victims of predators favor predator control, while those who are concerned with the survival of all species are opposed to it. Certainly predators help to maintain the natural population of prey species at the proper level in nature. When predators attack our livestock, we must weigh this damage against the damage to crops that could result from an increase in the predators' *natural* prey—mice, rats, and gophers, for example—if the predators were reduced. This, of course, is seldom considered. Any predator which even approaches the vicinity of livestock is likely to be destroyed, whether or not it has any evil intentions upon the livestock. The mouse-eating hawks of the genus *Buteo* are as severely persecuted as any predator, although it is well known that they rarely harm either livestock or game.

If, as a result of study of the ecology of the predator, it is decided to attempt to reduce its numbers, the problem remains—how? One method is the bounty system, which requires payment of a specified sum for each animal of a certain species that is killed. This system has seldom proved successful in predator control and it is costly; it also leads to widespread dishonesty and is very difficult to administer properly. Poisoning has been used but is dangerous to other species and even to humans in areas of heavy population. Fencing may protect livestock from certain predators, but this is often prohibitively costly and of course has no value for wild prey species. The use of biological controls, such as disease organisms and parasites, has not been established in the control of predators in this country, although it might be workable in some cases. The problem remains an enigma, but some solutions may be forthcoming with the increased study of this difficult question.

Habitat Improvement. Occasionally the availability of suitable habitat will limit the population of a game species. Attempts are then made to increase such habitats. In recent years, habitat improvement has proved to be one of the most effective tools in wildlife management. Many of our streams, for example, are not favorable for trout, which require a constant flow of cool water. By the placing of log dams or other devices to produce pools at intervals along shaded streams, trout habitat may be created (Fig. 11-16). Research may indicate whether or not the environment is suitable for a particular species and thereby save a great deal of effort and



William E. Werner, Jr.

Fig. 11-16 Trout stream improvement: by placing logs across the stream, conservationists have created pools which are favorable to trout.

money in management or stocking operations. In New York, the bobwhite quail is established in considerable numbers to make it available to sportsmen. Despite pressure for stocking upstate coverts, the conservation department has found that the winters of the northern part of the state will prevent the development of a population there. No restocking is attempted in that region (Smith, 1956).

Many more examples could be cited of the ways in which field biology is involved in the economics of our society. We must avoid, however, attempts to overstress the economic value of our natural resources and remember that in many ways the value of the organisms about us, with which the biologist works, is above any price that might be mentioned.

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chapter 12

The use of biological literature

To the professional biologist, close acquaintance with the literature of his sphere of interest is essential. To the amateur, it is often difficult to open the door to this strange never-never land of scientific writing, and many hesitate to attempt it. Admittedly, the literature of biology is complex; particularly it is difficult for the student to maintain touch with progress when he does not have access to a good library. Yet knowledge of the literature is so important that everyone interested in biology should make an effort to become familiar with the important publications in his own field.

TYPES OF BIOLOGICAL LITERATURE

The middle years of the twentieth century have seen the greatest proliferation of scientific literature that the world has ever known. Publications of importance to the biologist are pouring forth in English, German, Russian, Japanese, and a

Index learning turns no student pale,
Yet holds the eel of science by the tail.

Pope, "The Dunciad," Book I

variety of other languages. The time when a student could be expected to keep up with the important work by reading a few journals is past. Nor can he afford to ignore the work of any national group, lest he be duplicating work or otherwise wasting effort.

Although we cannot list here more than a sample of the many sources of biological information, we may be able to set up a few guideposts in the wilderness and point out a few of the necessary steps involved in a literature survey. We may begin with a consideration of the types of literature with which the field biologist must work.

We may classify sources of information into two groups —books and journals. Like most classifications, this is not a completely clear-cut division, but it will serve our purpose. Books are self-contained units, most often covering a single subject, frequently by a single author. They do not normally present previously unpublished data. Their function is rather to synthesize already published material, to analyze, to explain, possibly to theorize about the meaning of the data. Furthermore, books are always a year or two behind the times by virtue of the unavoidable fact that it takes time to prepare and print them. These two facts explain the necessity for journal literature and the biologist's concern with it.

Journals may be loosely defined as periodically published items with some sort of sequence and some sort of cohesiveness. This cohesiveness may be due to subject matter (*Journal of Genetics, Journal of Parasitology*); to the area covered (*Southwestern Naturalist, New York Fish and Game Journal*); to the publishing agency (*Proceedings of the Biological Society of Washington, Public Health Monographs*); or to some other unifying factor.

Journals, or more accurately serial publications, may be further separated into regular and irregular series. Most societies publish a regularly appearing journal. The Wildlife Society publishes its *Journal of Wildlife Management* four times a year. This is the most common pattern, but some, such as the *Journal of Parasitology*, appear six times a year, a few only twice. Many museums, state experiment stations, university biology departments, and other organizations publish a series which appears sporadically, whenever material and funds for publication are simultaneously available. The Illinois Natural History Survey, the National Museum in Washington, the American Museum of Natural History in New York, and a host of others publish such serials.

The number of scientific serial publications is enormous. *Biological Abstracts*, one of the leading publications which summarizes current literature, listed, in 1952, some 1,900 journals which were being reviewed. Since that time many more have begun publication. Quite obviously, the biologist cannot possibly digest even one-tenth of this quantity, unless he is independently wealthy and is willing to spend all of his time in a library. Yet he must keep abreast of developments, and in conducting research he must be able to find out what is known about his subject. Fortunately, a number of valuable and time-saving aids have been prepared for his use.

Reviewing the Literature

The purpose of a literature survey is to find out all that is known about your subject. Usually this is a preliminary to further research, which cannot be done effectively until the background reading has been done. Less commonly, the student may wish to learn what he can but does not intend to add to the knowledge of the subject himself. In our discussion of this subject, we shall mention most of the important sources of information, although the approach is somewhat different when one is browsing over current literature from when one is gathering references for a bibliography or literature review.

Let us consider first the manner in which a student might prepare a literature review about a particular subject in biology. The first step, and one which should be taken early in the career of the serious worker, is to secure and become familiar with a good book on the general principles of studying scientific literature. Such books as Trelease (1951), "The Scientific Paper," and Smith (1962), "Guide to the Literature of the Zoological Sciences," are invaluable to the student who wishes to learn to use the tools of his trade with proficiency. Such volumes will give a more complete and detailed discussion of the problems involved than can be given here in one chapter. In particular, they will point the way to publications with more specific information about the area of biology in which a worker is especially interested.

The next step is to secure a reference book which covers the general field in which the worker is interested and which includes a good list of references. A student of mammals might use Palmer's (1954) "The Mammal Guide," or the more recent texts by Cockrum (1962) and Davis and Golley (1963). A bird student might secure the proper volume of Bent's "Life Histories of North American Birds." In a reference of this kind, he would find a general survey of our knowledge as well as a list of references for further reading.

If the worker is unaware of any reference of this kind, he may find one listed in the "Publishers' Trade List Annual," and its index volumes. The Annual is arranged by publisher, the indices by author and subject. These volumes list all books currently available in America. They are issued annually, and are therefore as nearly as possible up-to-date. If it is necessary to seek books not currently in print the "United States Book Catalog" and the "Cumulative Book Index" may be used. These publications cover the years from 1928 to the present time and are available in most good libraries.

Bibliographies

Bibliographies are never really complete, but they are of great value, and there are hundreds of them in print. Indeed, there is at least one bibliography of bibliographies. Most branches of biology have been treated by bibliographers, though not in every case recently. Nonetheless, such classics as "A Bibliography of Birds," by Reuben Strong, and "Bibliography of Fishes," by Bashford Dean, are of tremendous value and should be familiar to every student in these fields. Often local or state bibliographies are available, such as Joseph Grinnell's "Bibliography of California Ornithology," and these are of special significance to the student of plant and animal distribution.

In many fields of biology, the worker is fortunate enough to have a colleague or a society which keeps an up-to-date bibliography of a particular field. Such is the Torrey card bibliography of botany, prepared by the Torrey Botanical Club since 1894. This card file is available in many libraries throughout the country. The few North American students of fleas are kept up to date by workers at the Rocky Mountain Laboratory at Hamilton, Montana. These Public Health Service employees maintain a continuing file of references to North American fleas and periodically publish an index which summarizes the literature up to that time. The worker who has not yet achieved familiarity with the literature of his field of interest could scarcely do better than to contact a competent authority who might direct him to an available bibliography. It is impossible to list here all of the many biological bibliographies which are available to the student, but a partial list is included in the Appendix.

The Reference File

When the student begins to use a bibliography or to seek specific references, he should begin to make notes for his future use. These notes may be kept conveniently on file cards; the 4- by 6-inch or 5- by 8-inch are preferable because more complete information can be kept on these larger cards. On each card, a full citation of the book or paper is written at the top. Often the student who is using a bibliography may wish to make out cards for a large number of publications which he has not yet seen. Unless this fact is indicated in some way, it may cause confusion at a later stage of the study, particularly if the card was filled with information about the article taken from an abstract journal. Some biologists put quotation marks or parentheses in pencil around the titles of articles which they have not yet seen, and then erase these marks when they actually read the reference concerned. This will prevent the unwitting copying of a quotation which one author has quoted from another, a practice which doubles the possibility of error. Every direct quotation should be taken directly from the original source, never cited from a copy in another article.

After the citation, which will include author, year of publication, title, and details of publication (Fig. 12-1), the biologist will write a brief summary of the article in question. The summary, or abstract, should be done with great care to include all the information which he is likely to need. Much valuable time may be wasted in going back to the same reference a second, third, and fourth time. Brevity and conciseness are important, but careful selection and absolute accuracy are essential. Direct quotations should be indicated as such, and it is wise to quote directly if there is a chance of misinterpretation.

From the papers cited in each article, the biologist will secure the names of other references. Eventually, this will lead to the necessity of a trip to a large library. The individual who is not connected with a large university or a museum will find it necessary to visit the nearest good library or to borrow a specific journal or two through an interlibrary loan system.

If it is necessary for the worker to travel some distance

Brockner, Winston W. 1954. Harris's sparrow in New York State.
Kingbird, 4(2):38.

Summarizes recent (since 1948) records of the species in the Northeast and records an immature from a feeding station at Hamburg, Erie County, Nov. 8 to 11, 1951. Bird was seen by several observers but was not collected. This is the seventh record from the Northeast since 1948.

Fig. 12-1 A citation of each pertinent paper with a brief summary of its main points should be kept on a file card.

to reach a good library, he would like to know in advance whether or not he can find the journals he needs there. He can learn what libraries have the journals he needs by checking the "Union List of Serials." This large volume lists all serial publications in the libraries of the United States and tells not only where they may be found, but the volumes available in each library (Fig. 12-2). Obviously, a list of this kind is never completely accurate, since accessions are constantly taking place; but it is a great help when one needs to locate an obscure journal or to check the holdings of a library which one plans to visit. It is also valuable to the student who

Novitates zoologicae (British Museum, Natural History)
London. v. 1–42, No. 3, 1894–Mr 1948 ||
1–41 published by Tring, Eng. Zoological Museum.
Suspended between 0 25 1940 and Mr 1948.
Superseded by the Museum's Bulletin. Zoology, 1950.

CCC 1–40
CLSU
CLU
CSt
CU
CU-A
CaT
DA
DLC [9,13,41–42]
DSI–M
ICF
ICJ
IU 1–[9]–42
IaAs
KU
KyU
LU
MB
MnU
NBuB
NIC
NN 1–15
NNM
NRU
OCL
OU
PPAP 7–[42]
PPi 7–[42]
TxHR
WaU

Fig. 12-2 Excerpt from the "Union List of Serials." The initials indicate the libraries which hold all or parts of this publication. For example, the University of California (CU) has the entire set, while the Carnegie Library at Pittsburgh, Pennsylvania (PPi) has only a partial holding.

wants to know the dates of publication of a particular serial or the exact name of a journal.

Now begins the laborious and time-consuming task of checking journals. It is wise to start with the journal which is likely to contain the largest number of references in your field of interest and to begin with the most recent issue and work backward. A good recent summary of the subject, if one has been published, will lighten the work load considerably by listing the more important publications and by pointing out the data which are needed.

The journal index is a good starting point. Comprehensive indexes are usually published at ten-year intervals, so that newer periodicals may not be included yet, but older journals may be indexed in one or several volumes. Each annual index, however, should be examined from the date of the last comprehensive index to the present.

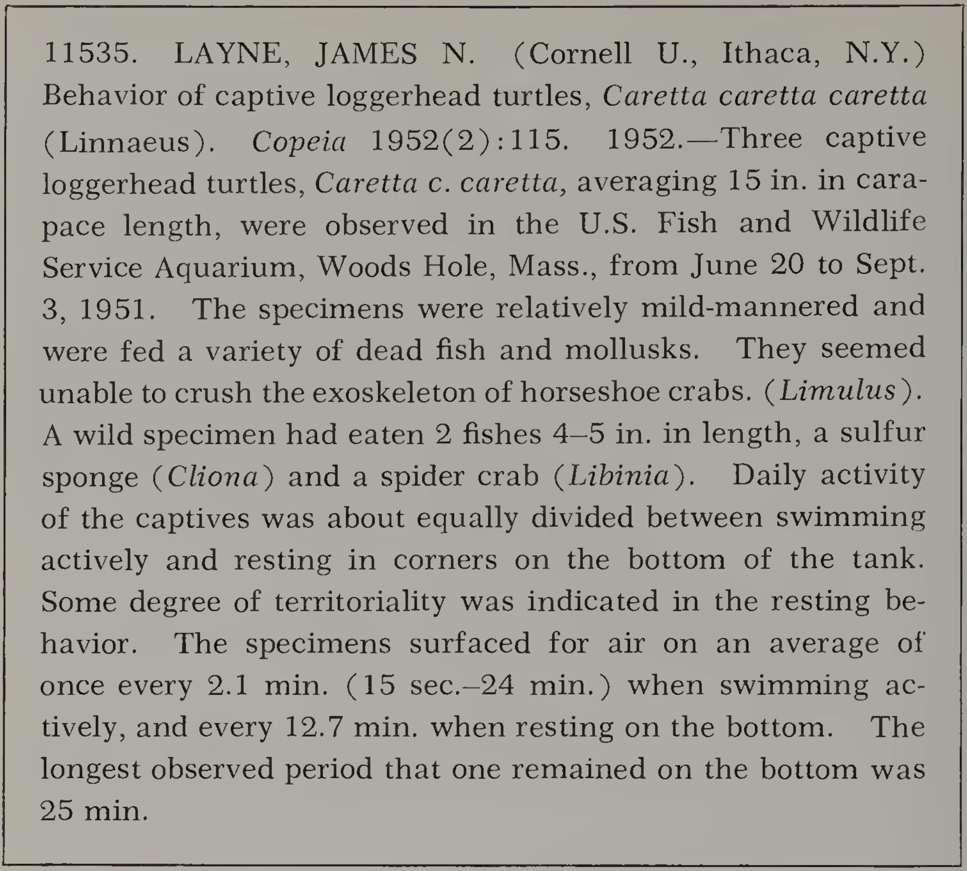
Journal examination is a snowballing operation, for each paper will list references and these will list others until eventually a rather complete bibliography is secured. When a biologist has checked several of the major journals in his field, he will probably have discovered more than half of the important papers.

Abstract and Bibliographic Journals

The examination of the abstract sources may precede or follow the examination of pertinent journals. Two of these bibliographic aids are of outstanding importance and will no doubt be the first two consulted: *Biological Abstracts* and *Zoological Record.*

Biological Abstracts is published monthly and includes, in most cases, brief summaries of papers which have appeared in several hundred journals (Fig. 12-3). Abstracts are grouped into sections, so that the user can examine only the areas which are of special interest to him. Currently there are four volumes per year, and abstracts generally appear within a year of publication. More recently, a “key word” listing known as B.A.S.I.C. has been added, and sections are now being published experimentally on microcards, which can be read with a dissecting scope or with a special microcard reader.

Biological Abstracts began in 1926 and is still being published. Its forerunner, *Botanical Abstracts,* covers the period from 1918 to 1925 and is of great value to botanists.



11535. LAYNE, JAMES N. (Cornell U., Ithaca, N.Y.) Behavior of captive loggerhead turtles, *Caretta caretta caretta* (Linnaeus). *Copeia* 1952(2):115. 1952.—Three captive loggerhead turtles, *Caretta c. caretta,* averaging 15 in. in carapace length, were observed in the U.S. Fish and Wildlife Service Aquarium, Woods Hole, Mass., from June 20 to Sept. 3, 1951. The specimens were relatively mild-mannered and were fed a variety of dead fish and mollusks. They seemed unable to crush the exoskeleton of horseshoe crabs. (*Limulus*). A wild specimen had eaten 2 fishes 4–5 in. in length, a sulfur sponge (*Cliona*) and a spider crab (*Libinia*). Daily activity of the captives was about equally divided between swimming actively and resting in corners on the bottom of the tank. Some degree of territoriality was indicated in the resting behavior. The specimens surfaced for air on an average of once every 2.1 min. (15 sec.–24 min.) when swimming actively, and every 12.7 min. when resting on the bottom. The longest observed period that one remained on the bottom was 25 min.

Fig. 12-3 A sample excerpt from *Biological Abstracts.*

Zoological Record is published by the Zoological Society of London, and is probably the most complete list of zoological publications in the world. It is, naturally, of no use in botanical problems as such. This publication does not include a summary of the material contained in each paper, as is done in *Biological Abstracts,* but merely lists the papers once and refers to them under several headings.

In order to use the *Record* successfully, it is necessary to understand something of the way in which it is organized. A section on comprehensive or general zoology is included at the beginning of each volume, listing papers which do not deal with any particular taxonomic group. After this, the arrangement is entirely phylogenetic—that is, it starts with the Protozoa and proceeds to the Mammalia, each paper within each phylum being given a number in sequence. The numbers begin with (1) in each section, since various specialists use the sections separately. Arrangement in each of the sections is alphabetical according to the last name of the author.

The worker who is searching for publications on a particular subject may not wish to search through the entire section for the few references which will interest him, and he may not know the names of the authors whose works he is seeking. For his benefit, a subject index lists the numbers of papers in each section, with the author's name, under such subjects as morphology, physiology, ecology, and others. A geographical index lists papers according to the region which they cover. This is followed by a systematic index, where each paper is listed according to the organism or group with which it deals (Fig. 12-4).

A special feature of the *Zoological Record,* of interest primarily to the taxonomist, is the list, at the end of each volume, of new generic and subgeneric names proposed during the year. In addition, new species and genera are listed under the section for each phylum, thus making it relatively easy for the taxonomist to find original descriptions of animals, as well as keeping him informed on the discovery of new species.

Although it is impossible for any such ambitious undertaking to be complete, each volume of the *Record* contains

Under *Insecta*—p. 62.
1122.—Fox, I. Notes on Puerto Rican mosquitoes, including a new species of Culex.—J. Parasit., Lancaster, Pa. 39:178–181, 1 pl. Dipt.
Under *Geography or Faunistic,* p. 276.
FOX, Mosquitoes, Porto Rico and Culex sp. n., 1122.
Under *Systematic*
Diptera, Culicidae, p. 438.
Mosquitoes of Porto Rico, FOX, J. Parasit. 39:178–179.
Culex, p. 439.
C. (Melanocorion) sardinerae sp. n., Porto Rico, p. 179, figs., FOX, J. Parasit. 39.

Fig. 12-4 Extracts from the *Zoological Record,* showing the manner in which an article is listed under various headings to facilitate use.

upwards of 15,000 references, making it one of the most comprehensive of all the bibliographies available to the zoologist.

The *Zoological Record* has the longest unbroken series of any important biological bibliography. It was started in 1864 and has been published more or less regularly since that time. It is usually only one to two years late in appearing; that is, the issue for 1952 might have been expected to appear in late 1953 or 1954. But the Second World War caused a delay of several years in publication of the series, and the volumes of the *Zoological Record* since that time have been three or four years behind.

A more recent publication, and one which keeps more nearly up to date than most such references, is the *Bibliography of Agriculture.* This important bibliography is prepared by the U.S. Department of Agriculture and is published monthly. Twice annually, in June and December, a summary index for the six-months volume is published. Although this bibliography is specifically concerned with agricultural publications, it contains much that is of value to every biologist. Its coverage of entomology is particularly good.

Because the *Bibliography of Agriculture* has world-wide coverage and because it is published at monthly intervals, it is an extremely valuable reference. Perhaps its greatest contribution is its complete coverage of publications of the U.S. Department of Agriculture and of the various state experiment stations.

Another relatively new publication is *Wildlife Review,* prepared by personnel of the U.S. Fish and Wildlife Service. This useful publication was started in 1935 and is published irregularly four or five times each year. Each issue includes brief abstracts of several hundred recent publications in the field of biology, listed according to subject matter and with an author index at the end. The coverage is extensive, though spotty, with the emphasis on articles and books related to wildlife management. The editors of the *Review* have been broadminded in their inclusion of material, however, so that this publication is indispensable to the worker in wildlife management and extremely useful to other biologists. One valuable contribution is its occasional listing of recent Russian publications, which are often unknown to American biologists. The only other source of adequate knowledge about these papers is the *Revue Zoologique Russe*, which has been published since 1920. This review, however, is in Russian.

In 1952, *Wildlife Review* items up to that year were assembled in a single volume. This book, titled "Wildlife Abstracts, 1935–1951," includes more than 10,000 items, arranged by subject matter as in the *Review*, but with a comprehensive index to facilitate its use. Two additional volumes now cover the literature through 1960.

The Quarterly Review of Biology is a journal devoted to reviews of recent books relating to the biological sciences. Each issue contains one or more scientific papers, but the larger part of the magazine consists of crisp, well-written reviews. No journal is more valuable to the student who does not wish to waste his time reading inferior books. Each issue reviews about a hundred recent publications, and many of the reviews are exceptionally complete. *The Quarterly Review of Biology* has been published four times each year since 1926.

Of less value to the professional biologist but useful to the person who wants to learn about popular articles on biological subjects is the *Readers' Guide to Periodical Literature*. Published monthly, the *Readers' Guide* first appeared in 1900 and is still in progress.

Some biological journals include in each issue an extensive list of recent articles in their field of specialization. Two such journals are *The Auk* and the *Journal of Mammalogy*. The student with a special interest in some limited area will find occasional helpful references in these lists, and may, if he desires, send for reprints of those which seem especially useful. Most authors (see p. 422) secure a number of copies of each publication which they have written and are willing to send a copy to anyone who asks for it. In many cases, this is the easiest way to secure access to a particular paper, if the journal in which it appeared is not readily available to the student.

With an extensive card file containing references to all major publications relating to his problem, a biologist is prepared to summarize existing knowledge and to recognize fruitful areas of research. Unfortunately, the literature search is so time-consuming that it is often carried on concurrently with research rather than in advance; but at least a preliminary survey of the more recent literature is essential to an understanding of any problem. Armed with the techniques and information contained in this chapter, the worker in biology should find it possible to proceed rapidly and confidently to make a reasonably thorough survey of literature in his field of interest.

REFERENCES CITED

With the exception of the following, the publications mentioned in this chapter are listed in the Appendix, pp. 425 to 462, along with other bibliographic, taxonomic, and scientific books and journals.

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Proc. Biol. Soc. Wash. 1880 and following. Published irregularly by Biological Society of Washington, Washington, D.C.
Readers' Guide to Periodical Literature. 1900 and following. Published monthly by The H. W. Wilson Company, New York.
Revue Zoologique Russe (Zoologicheskii Zhurnal). 1916 and following. Published in Moscow, U.S.S.R.

chapter 13

The choice and conduct of a field problem

The logical culmination of an interest in field biology is to choose and carry out a study of some aspect of the subject. Unfortunately, many well-trained and capable field workers never utilize their knowledge in carrying out a research project. Possibly many feel that they do not know how to set about it. Others may feel inadequate to choose and conduct a worthwhile problem. In most cases it is probably a matter of inertia, coupled with a feeling of inadequacy. This is especially true of those without formal training in field biology, though in many cases these persons may be as capable as most professionals.

It is the purpose of this chapter to encourage the beginner in field biology or the veteran field worker without research experience to attempt a field problem. No one should hesitate for fear that his contributions will be insignificant or that his work will be inadequate. We progress only by effort and experience, and though our progress may be slow, it will be nevertheless worthwhile.

Looking back, I think it was more difficult to see what the problems were than to solve them.

Charles Darwin, Letter to Charles Lyell, September 30, 1859

SELECTING A PROBLEM

The first difficulty involved in embarking on a study is the choice of a problem. Some people feel that all of the best problems have long ago been worked out. This is not true. In any area, no matter how well it has been studied, the field biologist can find many basic problems still untouched. The real difficulty lies in the selection. Of course, you cannot choose a problem unless you know what facts are missing in man's knowledge of the branch of field biology which interests you. Thus the literature survey must precede biological research. It may be this time-consuming and sometimes tiresome task which discourages many capable students from carrying on research. Unfortunately, there is no really satisfactory substitute for the procedure.

In reading about the subject which interests you, you may note that some particular pieces of information are lacking. If so, you already have the germ of a good problem. If not, read a good reference book (see Appendix) on the subject. Take notes on unsolved problems which are mentioned or on the areas in which no information is given. With these clues in mind, examine the major journals in the subject which have been published in the last two or three years. (It must be remembered that reference books are always two or three years behind current research.) If it appears after these surveys that several of the problems which you have listed remain unsolved, you have only to make the choice and begin your study.

The literature survey serves another purpose. While you are examining the books and journals to see what information is lacking, you should accumulate a good deal of material which will aid you in the pursuit of your problem. To organize such material, a card file of 5- by 8-inch cards should be set up, with a summary of each paper or of the pertinent information from each paper on a separate card (Fig. 12-1). These can be filed alphabetically by author, and will be of value throughout the progress of your problem and often for a much longer time. Special attention should be given to the techniques which you may use and to the manner in which the problems were approached and the data presented.

Selecting a problem may not weigh so heavily on the student, for whom ready-made projects are at hand. His adviser will often be able to find a part for him in a study already under way or will in other cases be able to suggest problems which he feels competent to supervise. In such cases, pertinent literature may be easier to get at, and the literature survey will be less onerous. Even so, the student will have to read and digest a good deal of material before he is ready to proceed.

The interested amateur, without ready access to an adviser or a library, may at this point throw up his hands and abandon the whole idea of research. This is not necessary. In almost every university there are field biologists who welcome the cooperation of willing helpers. The more remote your area is from such an institution, the more likely it is that it has never been thoroughly studied. After deciding upon a general area of interest, you may be able to contact someone at a nearby college, museum, or experiment station, who has knowledge of the literature and who can suggest areas in which information is lacking. If you are willing to collect specimens or data or make your observations available to the world in the best tradition of Gilbert White and other amateur naturalists, you may expect a certain amount of courteous guidance from a competent professional. Most such persons are willing to give suggestions as to what particular facts are lacking and to point out a method of approach which may be used. Such advice is always helpful, even though you may have been able to make a comprehensive survey of the literature for yourself.

Once the general area of study has been determined, it is necessary to fit the problem to your own personal requirements. This is the point where many fail. It is always intriguing to tackle the big problems requiring broad knowledge and deep insight, but most of us must content ourselves with simpler things. Before deciding upon a problem, see that it fits you in these five ways:

1. *It Must Fit Your Knowledge and Ability.* A beginning student in biology often suggests that he would like to experiment with such a project as the removal of the pituitary gland of a frog or rat and study the effects of such removal on the animal's behavior. He is usually hurt when it is pointed out that he has neither the knowledge nor the technical skill to perform the operation or to interpret the results correctly. A candidate for the doctorate in endocrinology might find such an experiment both practicable and interesting; the beginner would succeed only in slaughtering his subjects. Pick a problem which requires the skills you possess or can master in the time you have to give to the work.

2. *It Must Fit Your Facilities.* The worker who does not have unlimited space and unlimited funds must choose his problem carefully to utilize his available facilities to the best advantage. Caged animals require space, reasonably constant temperature and humidity, and good ventilation, as well as good care. Collections of most organisms take up space and require a certain amount of materials. Even the simplest field observations may require binoculars or other instruments. It is not necessary to give up, however, because of lack of materials. If you can secure a pencil and a notebook, and if you have time to give to your problem, you can make worthwhile studies. Before embarking on a problem, however, you must consider the facilities you will need.

3. *It Must Fit Your Time Schedule.* If your available hours are irregular, avoid the type of study which requires regular observations. If, on the other hand, you know that you will always be free at a particular time of the day, take advantage

of that fact by selecting a problem which requires daily observations. If your vacation coincides with a particular natural event such as bird migration, amphibian egg laying, or bat hibernation, some aspect of that event may be worthy of study. Whether small or large, the project must be one which can be adequately performed in the time you can give to it.

4. *It Must Fit Your Interests.* This may seem too obvious to require mention, but many people begin to work on a problem which is suggested to them, not because they have any personal interest in it, but because it looks as though it might yield results. Unless a worker is enthusiastic about a project and ready to submerge himself in it wholeheartedly, he is likely to get very tired of it before he is done. And worse yet, he is not so likely to do good work on a project which does not really interest him.

5. *It Must Fit Your Temperament.* We hear a great deal about the scientific temperament, but there are as many different temperaments among scientists as there are among businessmen or those in any other profession. Some scientists can work on a problem for many years, patiently accumulating data, as Darwin did to formulate the theory of evolution. Others like to see some results from their labors within a reasonable length of time. Some projects require extreme patience, as for example the study of a nesting bird, where long hours are spent in a blind. Other studies require extreme regularity and precision, as the gathering of data on light, humidity, changes in conditions at different times or seasons, and similar work. It may be true that a scientist must possess a consuming curiosity and the ability to do careful and accurate work. But within this framework, biology will offer a variety of projects, and you should choose one which will not prove unduly onerous. You will be very deeply involved with it for some time, and you should find it a source of continuing satisfaction.

Seeing the Problem

In the final selection of a problem for study, you must be particularly careful to avoid the "shotgun" type—one covering a great deal of territory but without a clearly defined aim. Your project should be precise. You should be able to state it in a single sentence, or at most in a short paragraph. The probable direction of your research should be clear to you at the start, and the results toward which you are aiming should be well defined. This is a part of "seeing the problem," and it is comforting to realize that such a great scientist as Charles Darwin had to resolve this difficulty. If you have an adequate grasp of the literature which concerns your problem, you will be able to formulate some promising approaches. Some of them will prove unfruitful and will be abandoned early in your work. Sometimes the answers to your questions will seem to elude your grasp as you come near them. But you are constantly assembling facts and accumulating knowledge and experience. Eventually, and in many cases with startling suddenness, the problem will spring into clear focus. You will be able to decide upon your best method of attack; to design the necessary experiments; to understand the relationship of your accumulated data to the total problem.

RESEARCH ON THE PROBLEM

The first step in the pursuit of research, once the problem is well defined, is the accumulation of data. In most problems in field biology, two types of data must be recorded: observational data and experimental data. The difference between the old natural history and the modern type of field biology lies largely in the use of experimental procedures by present-day workers. Nonetheless, much can be learned by careful observation and recording of data if a few precautions are taken.

Making Observations

An observer of wild animals, especially one without professional training, is likely to make the mistake of interpreting animal behavior in terms of his own mentality (see Chap. 10). This anthropocentric approach must be avoided. If interpretation of animal activities is to be made at all, it should be based on experimental work under controlled conditions, rather than on simple observations. Although, under ideal circumstances, biological observations should be made under natural conditions, this is not always possible. Field observations should be attempted first, and careful work will often solve most of the problems without recourse to an artificial environment.

The field worker, whether studying plants or animals, must use extreme care to ensure that his activities in the field do not affect the organism which he is studying. The use of an observation blind, left in place long enough to allow the animals to become accustomed to it, is often necessary for the student of birds and larger animals. Even more necessary in the study of animals is the ability to sit still; to move slowly; to ignore minor discomforts and annoyances. If the biologist lacks these attributes, it would be wise for him to confine his studies to organisms which do not need to be observed in this manner. Plants, of course, are not disturbed by the mere presence of a human observer; yet any disturbance of the habitat may affect certain plant species, and the student of plant ecology should be certain that his study areas are not affected by his activities.

Some Tools of the Field Observer

As with any science, field biology requires the student to be an inveterate note taker. No fact can be considered insignificant, though its significance may not be apparent at the time it is noticed. Key events, which may prove essential in the interpretation or understanding of a series of activities, are often missed unless one is especially careful in taking notes. This has led some field workers to depend upon the motion-picture camera for observations. Motion pictures are of undoubted accuracy, while recorded observations of the human eye are not. Pictures can be checked at a later date, at leisure, and under ideal conditions; notes must be taken at once and can be checked later only against the imperfect human memory. The speed of the camera can be varied to record movements quite unnoticed by the human eye. The development of high-speed and infrared films has made it possible to record events under conditions of very poor light. Furthermore, the moving picture is far superior to the written word in communicating to others the sequence of observed events.

Another modern device is rapidly taking its place in the battery of tools for the field biologist. This is the sound recorder, which is now available in a light, portable unit especially designed for field use. It records sounds of the animals being observed, and the observer, instead of writing field notes, may record his remarks as the activity is proceeding. Thus he does not need to take his eyes from the animals under observation, as he would have to do if he were writing. The recorder may note sounds which the observer misses, often sounds of critical importance. For an example of the use of the sound recorder in a field problem, you will find the paper by Frings et al. (1955) interesting and instructive.

The still camera, too, has been utilized extensively in field investigations, and can instantaneously record data which must otherwise be recorded laboriously in writing. The field biologist should learn to operate both still and motion-picture cameras effectively, as aids to his limited ability to translate visual images into writing. Further information on the use of these and other tools of the field biologist is given in the Appendix, pp. 444 to 453.

These instruments have disadvantages, to be sure. The noise of a camera, particularly of a motion-picture camera, may disturb some animals, especially when the instrument is used at close range. The operation of cameras requires some skill, which may involve the expenditure of a certain amount of time and money before proficiency is attained. Both camera and sound recorder are moderately expensive, and the fine instruments which are required for the most exacting field work are beyond the reach of many workers. For those with the means and skill to enjoy them, however, they may become exceedingly useful tools.

Recording Data

Whether the worker uses mechanical devices or simply a pencil and paper, it is important that all possible data be recorded. Memory cannot be trusted, especially for those small details which are so essential to accurate field observation. The collector must have full data on every specimen, as well as notes about weather, habitat, and other details. The botanist will need to record data on soil type, drainage, exposure, pH, and other factors affecting plant distribution. The entomologist must write an account of food plants, microecological distribution, daily activity cycles, and behavior. It has been said that note taking is a faultless pursuit, for it is seldom possible to take too many notes. It is true that a hundred pages of basic data may make a final report of only five pages when repetitions and disconnected or incomplete observations are eliminated and the rest is reduced to the shortest possible space. But at the time when notes are being taken, the note taker is in no position to evaluate the significance of any particular item or to check his past notes to see if he has made the same observation previously. It is better to have an unused wealth of field notes than to find the notes lacking in important points.

Experiments

Under some circumstances, field observations cannot reveal what we need to know, and organisms must be brought into the laboratory. Here, by duplicating natural conditions with painstaking thoroughness, we can vary certain environmental factors such as temperature, humidity, light, and habitat type, and learn how they affect the organisms. Behavior studies of animals, in particular, may require observation of captives, since many of the most important activities of animals are carried on at night or under cover. It is often possible to maintain untamed captive animals under such conditions that they will behave normally. Studies made on animals or plants under artificial conditions, however, are not necessarily indicative of the normal behavior of the same species in nature, and such observations should, whenever possible, be checked in the field. These studies will serve to answer many questions which cannot be solved by field work, however, since the animal or plant can be kept under close observation at all times. One could learn much of the mechanics of a diving bird's swimming or a fossorial mammal's digging by observations made of the animal in captivity in a glass tank of water or soil, while similar observations would be difficult or quite impossible in nature.

Laboratory observations, too, can be used to learn certain facts about organisms which could be learned in the field only by accident. How well can a certain animal swim? In nature, it would be unusual to observe most small mammals swimming. In captivity, one has but to place the animal in a tub of water, and the question is answered. Many other observations of this type may be made readily by study under controlled conditions.

Observational data, whether accumulated under natural conditions or in the laboratory, may not be sufficient to produce the needed information. The modern scientist, furthermore, is inclined to question the validity of observational data unsupported by experimental evidence. For this reason, it is often necessary for the field biologist to devise experiments which will support or disprove the hypothesis drawn from the data previously secured. In Chap. 1 we discussed briefly the use of the scientific method and the way in which it was used to solve a specific problem. We must now attempt to apply this method to field problems in general.

Setting Up the Experiment

The first requirement of an experimental setup is that it have a study population and a check population which are as closely similar as possible. The chemist may use identical test tubes and vary the contents in one component. Any difference in results may logically be considered a result of this component. The doctor of medicine gives identical-looking pills to all his experimental group, except that one section receives pills containing the medicine to be tested and the other section receives placebos, lacking this medicine. The field biologist must introduce this method into his studies.

When the biologist is working with captive animals or with greenhouse plants, the designing of experiments is usually not difficult. The total available population may be divided into as many groups as necessary, and the factors which are to be tested may be varied one at a time. The botanist may thus discover the ecological requirements of a plant species, its optimum soil type, its ability to survive within varying conditions of light, the amount of seed or fruit produced, and the conditions conducive to highest yield. All of these facts are significant in regard to the life of the plant and its relationship to the organic and inorganic environment. In the case of plants useful to man or to wildlife, these facts may have economic significance as well. Similarly, the zoologist may learn much about intraspecific and interspecific relationships of animals maintained under controlled conditions. The results of such experiments may aid the wildlife worker, the farmer, and the sportsman, as well as add to scientific knowledge.

If it is desired to set up experiments without resorting to artificial conditions, great care must be taken to choose two populations which are as nearly identical as possible. If a particular homogeneous area can be divided, one-half to be the experimental area and the other half to be the check area, this should be done. Experiments to test the effects of various chemicals, such as insecticides and weed killers, are usually set up in this manner. If such procedure is not possible, it is necessary to find a population of the organisms under consideration which is closely similar to the population of the experimental area. When the correlation between areas is not close with respect to populations, it is necessary to consider only those species common to both areas in order to arrive at acceptable conclusions. Such an arrangement is not ideal because the habitat itself presents another variable. The number of variables in experiments should be reduced to as few as possible, preferably to one. Thus any differences between the final status of the experimental population and the check population may be assigned a cause, with some assurance of accuracy.

Statistical Analysis

In many biological studies, it is difficult or impossible to set up experiments of the type required, yet the validity of one's conclusions must be checked in some way. Statistical analysis of data may be used in such cases to indicate whether the events recorded might have been accidental or were in all probability significant. In order to be suitable for statistical analysis, data must be such that they can be numerically expressed. Data on numbers of individuals per unit area, dimensions of organisms, and so forth, are susceptible to this kind of testing. The ramifications of this field are beyond the scope of the present book, though the worker with a sound knowledge of mathematics will find it easy to utilize statistics in his studies. Perhaps the best, or at least the easiest way for the student to learn about the use of statistics is to read a variety of papers in his field of interest. In this way he will see how data are analyzed, how statistics have been applied to a particular type of problem, and at least in general what formulas are used. He may not find a precise model for the kind of work he wants to do, but he will get some ideas. A group of such papers is listed in the Appendix, p. 456.

There are, in addition, a number of textbooks in which statistics are treated from the viewpoint of the biologist. A course in biological statistics or an understanding of one of the texts on the subject is essential to the well-trained biologist today. A few of the standard texts are listed at the end of this chapter.

Interpretation

Once the data have been gathered, experiments performed, and results analyzed, interpretation must begin. In purely observational studies, as indicated above, this may be impossible or at best tentative. Experimental and statistical data, however, will usually lend themselves to interpretation. Of course, experimental as well as observational data may be subject to misinterpretation. Some years ago an ecologist tested several species of small mammals to determine their water intake under uniform conditions in captivity (Odum, 1944). The object of the experiment was to determine the importance of water supply in the ecological distribution of these animals. The experiment was carefully designed, and the results were incontestable so far as the conditions of the experiment went. Water intake was found to agree with what was known about the ecological preferences of the various species. It would have been possible—indeed logical—to interpret these figures for water intake to indicate the actual water requirement of the animals. This, however, would have been a serious misreading of the data. Zoologists have maintained these same species in captivity for weeks or months without supplying any water, so long as abundant supplies of succulent food were offered. It is not unlikely that many small mammals in nature rarely drink water. This example serves to indicate that an extensive knowledge of natural history may serve a useful purpose in helping the student to understand and interpret experimental data.

The Law of Parsimony

On some occasions, data do not appear to fit any hypothesis, or, worse yet, appear to fit any of a number of hypotheses. The scientist, in such cases, is obligated to utilize the law of parsimony (sometimes called William of Occam's razor, after its originator). This principle requires that phenomena must be explained in the simplest terms and with the smallest possible number of concepts unless such an explanation can be proven to be erroneous. This generally accepted principle of logic, if adhered to, will prevent the worker from building complicated theories on insufficient data, although it may also result in an oversimplified explanation until further data are available.

PREPARING THE REPORT

If, after evaluation of the data, it appears that the study has produced results which may be of general interest, it is necessary to prepare the report for publication. Many workers are eager to publish their work—perhaps too eager; but other workers, including many capable amateurs, never publish anything. It is obviously unwise to withhold from your colleagues the results of your work if it can be of value to them. Publication entails a certain amount of trouble, but it is not a particularly complicated procedure. The first step in this direction is to choose the journal in which you wish your material to be published. An examination of journals in the field will give you an idea of the type of material which is acceptable to each. If the observations are primarily of local or regional interest, it may be best to publish them in a journal which confines itself to the biology of your area. A journal of national or international scope would not accept such material, but most states or regions have journals which specialize in local material. If, on the other hand, your research is of broad and general interest, it would be a mistake to publish it in a local journal, where it might escape the attention of many scientists who would find it important. In questionable cases, the editor of any journal can decide whether or not a paper is suitable for inclusion in its pages.

The editorial policy of the journal is usually stated in each issue, often inside one of the covers. Some journals have detailed explanations of how the manuscript should be prepared; others are less explicit. Because of the high cost of printing, authors are expected to utilize a sort of "law of parsimony" with regard to their writings. Tables and photographs especially are expensive to reproduce, and most journals place a limit on the number of plates that can be included. If the author feels that his material requires the use of numerous illustrations, he may be asked to share in the cost of printing them. To keep the size of the paper to a minimum, care should be taken to present data as briefly and simply as possible. All extraneous material should be deleted before the manuscript leaves the author's hands.

The best method of presentation of data will require some thought. Often graphs or charts will tell the story more succinctly than words. The use of photographs or other illustrations should be restricted to those which will show something not easily expressed in words and of importance to the report. Whether or not statistical analysis is required may present a problem. This question has been carefully treated by Stearman (1955) in a paper which should be read by those who prepare scientific papers.

Some skill is required to determine the type of material which is adapted to graphic presentation and to decide what form of presentation is most effective. Often it is necessary to prepare graphs and charts of different kinds, and then to choose the one which is best adapted to your purpose. If it is still not possible for you to decide the issue, the editor of the journal in which you plan to publish your paper may be able to give you advice.

Scientific Writing

Some scientists seem to labor under the illusion that a good scientific paper should be obscure, loaded with technical terms, verbose, and not understandable to the general public. In some cases this may be necessary, but it is by no means generally desirable. The scientific writer should make every effort to write as simply, precisely, and directly as possible. A book on style (Gunning, 1952) gives a yardstick to determine the complexity of a particular piece of writing. To determine what is called the *fog index,* average the number of words per sentence, or between major breaks within the sentence. Then calculate the percentage of words with three or more syllables, not counting capitalized words, word combinations, and multisyllable verb forms. Total the percentage thus arrived at with the number of words per sentence, and multiply by 0.4. This is the fog index, which is intended to indicate the approximate grade level in school which must be reached before adequate comprehension is possible. Popular writing, obviously, must have a fog index of 10 or lower. In technical writing, an index of 13 to 15 is perhaps allowable, but this is difficult reading. In general writing, such as in popular magazines, an index of 10 is usually maintained, even though many of these magazines have a large percentage of educated readers. Scientific writers may not be able to do so well, but the lower the fog index, the more understandable will be the writing. Of course, some technical terms must be used. This may render the paper unintelligible to those outside the author's field, but his colleagues will not be disturbed by such terms. The real test of a scientific paper is whether it is interesting and understandable to a majority of the author's colleagues. If not, it is unlikely to be a valuable contribution, unless its author is an Einstein.

Organizing the Paper

Another common fault of scientific papers is the failure to state, at the very beginning, what the paper is about. This should be done in the first paragraph. In suspense fiction, it is wise to retain some secrets from your readers until the final page, but in scientific writing this is not true. The author owes it to his readers to acquaint them at once with his intentions. It is not often that the title of a paper gives sufficient indication of its contents. It may catch the eye of the prospective reader, but if the first page or two of the paper should fail to enlighten him about its subject, he is justified in turning to the summary or in skipping the paper entirely.

Beyond this point, it is best to follow the prescribed practice of the journal for which you are writing. There is some variation in the manner in which the various parts of the paper are presented. In general, however, the paper should include at least the following sections:

1. *Introduction.* The problem is clearly stated and the background sketched in.
2. *Acknowledgments.* There is much variation in the exact placing of this paragraph, but almost every paper requires acknowledgment of the author's debts to those who have given him assistance.
3. *Methods and Materials.* Here you may outline the manner in which the problem was approached; the numbers and kinds of organisms with which you worked; the techniques you used, with reference to their source, and a description of any new techniques you may have developed; and any other information which may help the reader in understanding or evaluating your work.
4. *Results.* A brief statement of the conclusions of your research; it may include graphs and charts or simply tell what you found out about the problem by the use of your particular approach.
5. *Discussion.* It is often necessary to compare the results of your work with those of previous workers or to explain and interpret your results. This may be the bulk of your paper, or, if your results are largely self-explanatory, the discussion may be very brief. It is an extremely important part of your paper, because it is here that you show your understanding of the scope of the problem and the meaning of your research.
6. *Summary or Abstract.* A short summary of the paper, in some journals placed at the beginning and in others at the end, serves two purposes. It will be of value to the person who does not have the time or interest to read the entire paper, and it provides a summary of the main points for those who have read it. If the paper is to be published in a journal whose

contents are cited in *Biological Abstracts*, the summary of the paper may be similar to the abstract which the author prepares.

7. *Literature Cited.* Most American journals have now adopted the method of citation recommended by the "American Institute of Biological Science Style Manual" (see reference at end of chapter). The author should check the directions for authors in the journal for which he is writing and follow them carefully. Unless your paper is an exhaustive monograph, literature references should include only those which are directly pertinent. This is not a bibliography but only a list of references which are actually mentioned in the body of the paper.

In the case of short notes, the above division may not be necessary. These brief notes present the observations or the experimental results in a clear, direct manner, and literature citations are usually embodied in the text in abbreviated form. Again, the best guide is a study of the journal in which the paper is to be published.

If it is at all possible, the manuscript should be read critically by at least one competent authority. Of course, this will be done eventually when you send it to an editor. But many of the faults of a manuscript can be corrected before the editor sees it if someone other than the author reads it.

From Manuscript to Printed Page

When the manuscript is completed and typed in accordance with the requirements of the journal, it is sent to the editor. He will usually acknowledge receipt of the manuscript at once, although it may be some time before he reads it or sends it to an associate editor for reading. After this is done, he is likely to return it to you with suggestions for improvement. Authors are sometimes upset because editors edit. This, however, is their function, and they are generally chosen because they can do it well. A good editor may be able to cut a manuscript nearly in half without markedly reducing its value. He will not usually do this cold-bloodedly, however. He is more likely to ask the author to cut and to make suggestions which will help in doing so. If the paper contains too many tables or plates, the author may be asked to eliminate some of them. The requirements with regard to tables and plates are usually stated in the journal, and the author is expected to abide by these rules or pay for the difference.

The time between the submission of a paper and its appearance in print may vary a great deal. It depends upon the number of papers which are submitted to the editor, the amount of money available, the importance of your research, and other factors. In general, six months to a year may elapse between submission and appearance of a paper. In some journals, longer and more important papers are published sooner than short research notes, while in other journals the reverse is true. This time lag between completion of research and publication of results is unfortunate, but there seems to be no way to avoid it. Some journals are more prompt in publication than others; some have larger backlogs of material. But all are dedicated to the task of publishing original papers as rapidly as possible. The author should realize this fact and be tolerant of unavoidable delay.

Galley Proof

Some months after acceptance of your paper, the editor will send the galley proof for correction. This will probably be the last time you will see your paper before it appears in the journal, so you must be certain that mistakes, at this point, are kept to a minimum. This is not the time, however, for major overhauls of the manuscript or for insertion of afterthoughts. Resetting of type is expensive, and changes which will involve more than one or two lines may have to be paid for by the author. If there is an error in the way your original material was set, and this is the fault of the printer, he will correct it, but he cannot be expected to make major revisions of the material after the proof has been set. Typography, spelling, capitalization, plate descriptions, and numbers should be carefully checked. The printer or editor will supply you with a guide to printers' signs. There may be some of these marks on the proof when you receive it, since the editor may have had an opportunity to check it for obvious errors.

It is the duty of the author to check and return the proof promptly. Most editors expect that the proof will be retained in the hands of the author for no more than 24 hours. This may seem rather exacting, but editor and printer are operating on an exacting schedule. They must have cooperation from authors if they are to publish their journal on time.

Reprints

With the proof, the author may receive several other items. One is a reprint order. Most journals nowadays do not furnish free reprints, although some retain this practice. Some give a number of free copies if a certain minimum number is ordered by the author. These reprints are purchased by the author in order that he may have copies of his paper to give to his friends and colleagues and to the many interested persons who, he hopes, will want one. Such demands are not generally large, but they provide a means of interchange of information among scientists. A worker who does not have access to a large library and who cannot afford all the journals he needs may compensate to some degree by requesting reprints in his particular field of interest. A reprint file, properly indexed, may be a great timesaver for any biologist.

Another enclosure, along with the proof, may be the form for submission of a brief summary of the paper to *Biological Abstracts*. Since this abstract journal is used throughout the world, the abstract must be written with the greatest care. General directions are given on the form, but the author must take the responsibility for reducing the meat of his research to a few words. This abstract may be the only form in which his paper will be read by many interested people, and it will be used for many years. The art of abstracting is not an easy one, and the job should not be done hurriedly.

With the proof returned to the printer, the author has only to wait for the appearance of his paper in the journal. His reprints will be sent from the printer a week to a month after the paper is published, and the abstract of the paper will appear in *Biological Abstracts* from six months to a year later.

The many details involved in getting one's research published should not discourage the student of field biology. One does not need to be a professional biologist to contribute much that is worthwhile, and many amateurs have become world authorities. The late Baron N. C. Rothschild, of the British banking family, was one of the world's foremost authorities on fleas. Margaret M. Nice was an amateur observer of birds who became one of the most capable students of bird behavior and a world-recognized authority. Her early investigations were performed largely in her own dooryard. There is always room for excellence, whether it is amateur or professional. The edifice of scientific knowledge contains many small stones of information. It is to the further growth of this edifice that all scientists, amateur and professional alike, are dedicated.

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Appendix

The biologist, like scholars of all disciplines, finds that books are among his most important tools. The book lists given here, however, are not intended to be complete. Emphasis is given to books which are useful for identification of organisms and to books which can be read without extensive biological training. In areas where such volumes are not yet obtainable, we have recommended some relatively technical works. The brief review following each title will indicate the degree of difficulty of each book.

In most cases, we have chosen books which are still in print and thus available to the student who may wish to own a copy. Some particularly valuable works have been included in spite of their age, and such books may be available from a public library or from a dealer in secondhand books. Unfortunately a highly regarded book, when it goes out of print, often commands a price far above its original cost. Copies of the first volume of Bent's "Life Histories of North American Birds," for example, cost 50 cents when published. In recent years good copies have brought as much as $30 or $40. Obviously such publications can be purchased only by the student with unlimited funds or by bibliophiles. Fortunately, some classics like this are now being reprinted.

Many publications, however, are printed by an agency which sells them at cost, and the alert student may secure these books upon publication at a nominal price. For this reason we have included a brief list of some of the more important sources of biological literature of this type. The average amateur biologist may discover little of interest here; but the professional or the more serious amateur will find it essential to secure familiarity with this category of biological literature.

In addition to the lists of books, we have included a list of journals which are of particular importance to the biologist, together with the respective publishers' names. For a more complete list of such publications, the reader should refer to *Biological Abstracts,* vol. 26, May, 1952.

A list of important bibliographical tools is also included for the benefit of the serious student. The list is, again, incomplete but will serve as a point of departure in the preparation of a bibliography.

The second part of the Appendix is concerned with tools and materials which the field biologist must use. This brief discussion is included in the hope that it will be of assistance to the beginner or amateur in choosing the instruments he will need in the pursuit of his studies. For those whose interest leads to a desire for further knowledge, a list of publications on techniques is included, along with lists of sources for many different kinds of biological materials and instruments.

BOOKS FOR THE FIELD BIOLOGIST

Lower Plants

Bodenberg, E. T. 1954. "Mosses: A New Approach to the Identification of Common Species." Burgess Publishing Company, Minneapolis. The author of this semipopular guide to common mosses has attempted to correct the faults of earlier guides and to make his book easier to use and more valuable to the nonprofessional. The illustrations are abundant and clear, the keys good.

Chapman, V. J. 1962. "The Algae." Macmillan & Co., Ltd., London. St. Martin's Press, Inc., New York. A technical book, but well illustrated and containing a wealth of information on algae. Identification to families and genera.

Cobb, Boughton. 1956. "A Field Guide to the Ferns." Houghton Mifflin Company, Boston. The fern guide in the Peterson series; this is an inclusive little volume which covers ferns and fern allies of the eastern half of the United States. Specialists have added material about how to grow ferns, the history of ferns, and other such information.

Conard, H. S. 1956. "How to Know the Mosses." William C. Brown

Company, Dubuque, Iowa. A moderately technical book, designed only for identification; depends upon keys with each character illustrated; one of the Pictured-Key series.

Dawson, E. Yale. 1956. "How to Know the Seaweeds." William C. Brown Company, Dubuque, Iowa. Although this book is moderately technical, the excellent line drawings make identification relatively easy. It is primarily taxonomic but does include information on vegetative and reproductive structure and methods of collecting and preserving seaweeds.

Fergus, Charles L. 1960. "Illustrated Genera of Wood Decay Fungi." Burgess Publishing Company, Minneapolis. One of several technical books on the seldom-treated groups of fungi. Intended for textbook use in specialized courses in plant pathology.

Fink, Bruce. 1960. "The Lichen Flora of the United States." The University of Michigan Press, Ann Arbor, Mich. Published originally in 1935, this volume is still a useful book, especially to the professional botanist or serious student of lichens.

Krieger, L. C. C. 1947. "The Mushroom Handbook." The Macmillan Company, New York. A popular guide to the more common species of higher fungi. The illustrations are good, and the species included are those most generally common. More inclusive local guides may be needed for the more advanced student.

Nearing, G. G. 1962. "The Lichen Book." Eric Lundberg, Ashton, Md. Few scientists work on the lichens, and even fewer write popular guides. This thick book is an adequate and easily used guide with keys based on visible structural characteristics. Each species is illustrated.

Prescott, G. W. 1954. "How to Know the Algae." William C. Brown Company, Dubuque, Iowa. A semipopular guide using the Pictured-Key approach. Less inclusive and less technical than the book by Smith (see entry following).

Smith, Gilbert. 1950. "The Fresh-water Algae of the United States." 2d ed. McGraw-Hill Book Company, New York. Although technical in treatment, the book contains excellent illustrations, which make it valuable to anyone who studies algae. This is the standard technical reference on American algae.

Taylor, W. R. 1957. "Marine Algae of the Northeastern Coast of North America." 2d ed. The University of Michigan Press, Ann Arbor, Mich. (see entry following).

———. 1960. "Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas." The University of Michigan Press, Ann Arbor, Mich. These two books are the standard technical references for marine algae of the Atlantic coast.

Wherry, E. T. 1961. "The Fern Guide." Doubleday & Company, Inc., Garden City, N.Y. One of the best guides to ferns and fern allies. Concise but complete information on many aspects of fern life.

Wildflowers

Abrams, LeRoy. 1923, 1944, 1951, and Roxana S. Ferris. 1960. "Illustrated Flora of the Pacific States." Vols. I–IV. Stanford University Press, Stanford, Calif. A technical work, but it contains a description and illustration of every species of wild fern, herb, tree, and shrub in Washington, Oregon, and California.

Cuthbert, Mabel. 1949. "How to Know the Spring Flowers." William C. Brown Company, Dubuque, Iowa (see entry following).

———. 1948. "How to Know the Fall Flowers." William C. Brown Company, Dubuque, Iowa. These two Pictured-Key guides cover the most common flowers of the United States east of the Rocky Mountains.

Davis, Ray J., John J. Craighead, and Frank C. Craighead, Jr. 1963. "A Field Guide to Rocky Mountain Wildflowers." Houghton Mifflin Company, Boston. A Peterson guide which describes 590 of the 5,000 species of plants of this area, 209 illustrated in color, 118 by drawings. A technical key is included.

Fassett, Norman C. 1957. "A Manual of Aquatic Plants." Rev. ed. The University of Wisconsin Press, Madison, Wis. This is a technical book with keys to species, but illustrations are good and allow accurate identifications to be made.

Fernald, M. L. 1950. "Gray's Manual of Botany." 8th ed. American Book Company, New York. The classic of American technical botany manuals has been brought up to date in this large volume. It is not suitable for the beginner in botany, but for the serious student it is excellent.

Gleason, H. A. 1952. "The New Britton and Brown Illustrated Flora of the Northwestern United States and Adjacent Canada." 3 vols. Published by the New York Botanical Garden, New York. Like Gray's manual, Britton and Brown's work has long been used by American botanists. This latest edition is thoroughly revised. The illustrations make this somewhat easier to use than Gray's manual, but it is larger and more expensive.

Gleason, H. A., and Arthur Cronquist. 1963. "Manual of Vascular Plants." D. Van Nostrand Company, Inc., Princeton, N.J. This is essentially a one-volume condensation of the previous volume without the illustrations.

Matthews, F. S. 1955. "Field Book of American Wild Flowers." Rev. ed. Edited by Norman Taylor. G. P. Putnam's Sons, New York. For many years a leading popular guide; the latest edition is a modern, well-illustrated guide, one of the best of its kind.

Munz, Philip A. 1961. "California Spring Wild Flowers." University of California Press, Berkeley, Calif. (see entry following).

———. 1962. "California Desert Wild Flowers." University of California Press, Berkeley, Calif. (see entry following).

———. 1963. "California Mountain Flowers." University of California Press, Berkeley, Calif. These three popular guides by a professional botanist are an outstanding example of a good, usable guide to the most commonly encountered flowers of a region. The books are well illustrated, and the simple color key easy to use.

Munz, Philip A., and David D. Keck. 1959. "A California Flora." University of California Press, Berkeley, Calif. A more complete treatment of the flora of California. Species are grouped in a modern treatment, according to the plant communities in which they are usually found.

Pohl, Richard W. 1954. "How to Know the Grasses." William C. Brown Company, Dubuque, Iowa. A Pictured-Key series book on this difficult but interesting group of plants. The illustrations make identification easier than is the case with more technical works.

Wherry, E. T. 1948. "The Wildflower Guide." Doubleday & Company, Inc., Garden City, N.Y. Covering the East and Midwest, this handsome little book features excellent illustrations, half of which are colored, and

half are line drawings. Hints on culture of the plants in wildflower gardens are included. Introduced plants are covered separately from native plants; this often requires the user to look in two places to identify a particular plant.

Trees and Shrubs

Baerg, Harry. 1955. "How to Know the Western Trees." William C. Brown Company, Dubuque, Iowa. A Pictured-Key to the trees of the Pacific and Rocky Mountain states. Format identical to other books in this series.

Harlow, William M. 1942. "Trees of the Eastern United States and Canada." McGraw-Hill Book Company, New York. One of the best pocket guides to trees. Pictures are good; discussions of each species are thorough. Designed for the person without professional knowledge of forestry. A reprint edition is available from Dover Publications, Inc., New York.

Harrar, Elwood S., and J. George Harrar. 1962. "Guide to Southern Trees." 2d ed. McGraw-Hill Book Company, New York. For naturalists south of the Mason-Dixon line, this pocket-size guide will prove extremely useful. It is similar in format to Harlow's book, well illustrated and popularly written.

Graves, A. H. 1956. "Illustrated Guide to Trees and Shrubs." Harper & Brothers, New York. Probably the best available guide for the Northeast; beginners find this book among the easiest to use, and it is a valuable reference for the more skilled.

Jaques, H. E. 1946. "How to Know the Trees." Rev. ed. William C. Brown Company, Dubuque, Iowa. The companion volume to the book by Baerg, above. It covers the area east of the Rockies.

McMinn, Howard E., and Evelyn Maino. 1956. "Illustrated Manual of Pacific Coast Trees." University of California Press, Berkeley, Calif. The title of this regional guide is self-explanatory.

Petrides, George. 1958. "Field Guide to the Trees and Shrubs." Houghton Mifflin Company, Boston. One of the Peterson field-guide books, it covers trees, shrubs, and vines of northeastern and central North America, with illustrations for 639 species.

Preston, Richard J., Jr. 1940. "Rocky Mountain Trees." Iowa State College Press, Ames, Iowa. Covers the states of Idaho, Montana, Wyoming, Nevada, Utah, Colorado, Arizona, New Mexico, and western Texas. Good keys, illustrations of each species, and range maps are useful features.

———. 1960. "North American Trees." Rev. ed. The Iowa State University Press, Ames, Iowa. The format of this book is the same as the one above. Both books are attractively presented and well written.

United States Department of Agriculture. 1949. "Trees: Yearbook of Agriculture." U.S. Department of Agriculture. A compendium of information about American trees; authorities in all phases of forestry, in and out of the Department, collaborated in writing this large book. One section deals with North American trees, species by species, with illustrations showing the outstanding characteristics of each. Other sections include tree diseases, forest insects, forest wildlife, and many other items which make this an outstanding reference book for anyone interested in American forests.

Vines, Robert A. 1960. "Trees, Shrubs, and Woody Vines of the Southwest." University of Texas Press, Austin, Tex. Detailed information including illustrations for over 1,200 species, written with a minimum of technical terms.

Invertebrates

GENERAL:

Barnes, Robert D. 1963. "Invertebrate Zoology." W. B. Saunders Company, Philadelphia. An excellent, modern textbook on invertebrates, written for students having a year's training in college biology.

Buchsbaum, Ralph. 1948. "Animals without Backbones." Rev. ed. The University of Chicago Press, Chicago. This semitechnical discussion of invertebrates is a widely used text but may be read profitably by those with little biological training. Illustrations are abundant and good.

Carson, Rachel. 1955. "The Edge of the Sea." Houghton Mifflin Company, Boston. A popular account of the common organisms along the Atlantic coast, written in a graceful style.

Edmondson, W. T. (ed.). 1959. "Ward & Whipple's Fresh Water Biology." John Wiley & Sons, Inc., New York. This new edition of a classic in its field has been extensively revised. It is a technical work but should be of use even to a beginner.

MacGinitie, G. E., and Nettie MacGinitie. 1949. "Natural History of Marine Animals." McGraw-Hill Book Company, New York. A general natural history survey of marine invertebrates, with special reference to the Pacific coast of California. Persons without extensive biological training can read it with interest and understanding.

Miner, Roy W. 1950. "Field Book of Seashore Life." G. P. Putnam's Sons, New York. Covers the coastal area from New England to North Carolina. The pocket-size format makes it a good, handy book for field use, although the nomenclature is badly out of date.

Pennak, Robert. 1953. "Fresh-water Invertebrates of the United States." The Ronald Press Company, New York. A massive and concentrated volume, with keys to fresh-water invertebrates as well as detailed discussions of their ecology, anatomy, and physiology. A technical reference of great value.

Pratt, H. S. 1953. "Manual of the Common Invertebrate Animals." McGraw-Hill Book Company, Blakiston Division, New York. This re-issue makes available once again a standard reference work on invertebrates. It covers all groups except insects; treatment is moderately technical.

Ricketts, E. F., and Jack Calvin. 1952. "Between Pacific Tides." 3d ed. Revised by Joel Hedgpeth. Stanford University Press, Stanford, Calif. The common animals of the Pacific seashore are included in this popular guide. The Appendix provides an exceptionally complete list of literature, with notes about each item included.

PROTOZOA:

Jahn, T. L. 1949. "How to Know the Protozoa." William C. Brown Company, Dubuque, Iowa. Because of the extensive use of pictures in the Pictured-Key series, this is one of the few books which the beginner can use with reasonable effectiveness. It includes the more common species of Protozoa found in eastern North America.

PARASITES:

Chandler, Asa. 1961. "Introduction to Parasitology." 10th ed. John Wiley & Sons, Inc., New York. Among the most popular texts in parasitology, this book is rather technical. The most recent edition presents up-to-date information which can be read profitably by anyone with a background of college zoology. For more popular treatment, the following book is more suitable.

Rothschild, Miriam, and Teresa Clay. 1952. "Fleas, Flukes, and Cuckoos." William Collins Sons & Co., Ltd., London. (In U.S., Philosophical Library, Inc., New York.) Despite the incongruous title, this volume covers the subject of parasitology with special reference to birds in a most refreshing and interesting manner. The amateur is not burdened with a large number of text references, footnotes, and such items, but an appendix covers the literature very thoroughly for those who wish such information. The illustrations are excellent.

MOLLUSCA:

Abbott, R. T. 1954. "American Seashells." D. Van Nostrand Company, Inc., Princeton, N.J. One of the New Illustrated Naturalist series, this volume has the beautiful illustrations which are characteristic of the series. More than 1,500 species of marine mollusks are discussed and illustrated.

Keen, A. Myra. 1963. "Marine Molluscan Genera of Western North America." Stanford University Press, Stanford, Calif. Contains a workable key as well as ecological information and a systematic list.

Morris, Percy. 1939. "What Shell Is That? A Guide to the Shell-bearing Mollusks of Eastern North America." Appleton-Century-Crofts, Inc., New York. This is a popular guide to the more common land and fresh-water mollusks. About 75 species are included with good illustrations.

———. 1951. "Field Guide to the Shells of Our Atlantic and Gulf Coasts." Houghton Mifflin Company, Boston (see entry following).

———. 1952. "Field Guide to the Shells of the Pacific Coast and Hawaii." Houghton Mifflin Company, Boston. These two volumes in the Peterson series permit identification of marine mollusks along our entire coastline. They are beautifully illustrated and authentic.

Pilsbry, Henry A. 1939–1948. "Land Mollusca of North America." 4 vols. Academy of Natural Sciences, Monograph 3, Philadelphia. A technical work on land mollusks but with abundant illustrations which may make it useful as a reference for nonprofessionals.

SPIDERS:

Cloudsley-Thompson, J. L. 1958. "Spiders, Scorpions, Centipedes, and Mites." Pergamon Press, New York. Not a book on identification but on modern ecology and natural history of this group of animals.

Comstock, J. H. 1940. "The Spider Book." 2d ed. Rev. ed. Edited by W. J. Gertsch. Doubleday & Company, Inc., Garden City, N.Y. The classic among popular books on spiders, this large and handsome volume is one

of the most useful references for this group. It contains a wealth of information about the biology of spiders and serves as an identification manual as well.

Gertsch, W. J. 1949. "American Spiders." D. Van Nostrand Company, Inc., Princeton, N.J. This New Illustrated Naturalist volume is a beautifully produced book on the ways of spiders, not specifically designed for identification, but with illustrations which will, nonetheless, permit identification of many species.

Kaston, B. J., and E. Kaston. 1953. "How to Know the Spiders." William C. Brown Company, Dubuque, Iowa. For the Pictured-Key book on spiders, the authors have done a difficult job well. The more common of the thousands of species of spiders are included, with clear drawings illustrating the technical points of distinction. Because of the tremendous number of species and the difficulty of identification, spiders do not lend themselves well to a popular book or key. In this book, however, the keys are good.

INSECTS:

Among invertebrates, the insects enjoy the same degree of popularity which birds enjoy among the vertebrates. For this reason, there is a wealth of material on this group, both popular and technical. Only a few of these works can be included here, but the popular guide by Swain (1948) includes a good list for the beginner.

Borror, D. J., and D. M. DeLong. 1964. "An Introduction to the Study of Insects." Rev. ed. Holt, Rinehart and Winston, Inc., New York. A modern textbook of entomology, well illustrated and only moderately technical.

Chu, H. F. 1949. "How to Know the Immature Insects." William C. Brown Company, Dubuque, Iowa. Immature insects are singularly difficult to identify, but this book, by one of the few authorities on this subject, is a very adequate treatment of a difficult field. Most immature insects can be placed in the proper order and family by the use of the well-illustrated keys.

Essig, Edward O. 1958. "Insects and Mites of Western North America." 2d ed. The Macmillan Company, New York. A textbook of entomology emphasizing the western part of the country, on a rather technical level.

Imms, Augustus Daniel. 1951. "Insect Natural History." William Collins Sons & Co., Ltd., London. (In U.S., McGraw-Hill Book Company, Blakiston Division, New York.) One of the New Naturalist series, this outstanding volume has a most interesting and readable text and some of the most beautiful colored photographs of insects ever published. Not an identification manual, it discusses the lives of insects in an absorbing and well-organized manner.

Jaques, H. E. 1947. "How to Know the Insects." William C. Brown Company, Dubuque, Iowa. A Pictured-Key book, designed as a key to insect families. Comparatively nontechnical.

Klots, A. 1951. "Field Guide to the Butterflies." Houghton Mifflin Company, Boston. A model field guide, with brief but adequate introductory material, beautiful illustrations, and a clear, concise text. One of the Peterson series, it is outstanding.

Lutz, Frank. 1935. "Field Book of Insects." 3d ed. G. P. Putnam's Sons, New York. An excellent though old reference. Coverage is more extensive than is usual in popular guides, and the book is interestingly written.

Swain, Ralph. 1948. "The Insect Guide." Doubleday & Company, Inc., Garden City, N.Y. One or two important species in each of the larger families of insects serve as examples in this beautifully illustrated book. The list of references makes this good field guide even more useful.

Usinger, Robert L. (ed.). 1956. "Aquatic Insects of California, with Keys to North American Genera and California Species." University of California Press, Berkeley, Calif. Although the keys are usable only to genera outside of California, this handsome, large volume is still highly useful throughout the United States. It is a technical book but contains many superb illustrations which make the book useful even to the beginner.

Vertebrates

GENERAL:

Blair, W. F., A. P. Blair, P. Brodkorb, F. Cagle, and G. A. Moore. 1957. "Vertebrates of the United States." McGraw-Hill Book Company, New York. The only book in print containing keys to all the vertebrates of the United States. The keys are technical, and most species are not illustrated. Only taxonomic features and pertinent information such as range of species are given. Since many of the popular guides, such as the Peterson series, do not have keys, this book can serve a useful function in differentiating difficult species.

FISHES:

Breder, Charles M. 1948. "Fieldbook of Marine Fishes." G. P. Putnam's Sons, New York. The keys are difficult, and the nomenclature out of date. However, most of the species are illustrated with line drawings, and additional halftones are included in the back of the book. Coverage is the Atlantic and Gulf coasts.

Eddy, Samuel. 1957. "How to Know the Freshwater Fishes." William C. Brown Company, Dubuque, Iowa. Once again, the Pictured-Key series makes identification of a difficult group much easier with illustrations.

Harlan, J. R., and E. B. Speaker. 1956. "Iowa Fish and Fishing." 3d ed. Iowa Conservation Commission, Des Moines. Although this is a state publication, it is the most generally useful volume on fishes of the Midwest. The third edition has ironed out the few faults of the earlier ones, and the colored plates are available separately and are a remarkable example of color reproduction.

Hubbs, Carl, and Karl Lagler. 1960. "Fishes of the Great Lakes Region." Cranbrook Institute of Science, Bulletin no. 26, Bloomfield Hills, Mich. The outstanding guide to eastern fishes; fairly technical, but the terms are described and illustrated in full, so that the keys run fairly easily after the reader gains some experience with them. Clear diagrams of the diagnostic points will help the beginner learn the necessary technical details. A few good color plates are included, but most species are shown only in halftones from photographs. Since the book includes all of the waters of the Great Lakes drainage, most of the species which occur in the East are included.

Lagler, Karl F., John E. Bardach, and Robert Miller. 1962. "Ichthyology." John Wiley & Sons, Inc., New York. A textbook on ichthyology, summarizing modern knowledge on the subject. Not a key.

LaMonte, Francesca. 1945. "North American Game Fishes." Doubleday & Company, Inc., Garden City, N.Y. A well-illustrated guide to game fishes, both fresh-water and marine; of special interest to the sportsman are record catches for each species. Many attractive colored plates and a unique key are features of this pocket guide.

Norman, J. R. 1963. "A History of Fishes." 2d ed. Revised by P. H. Greenwood. Hill & Wang, Inc., New York. This is perhaps the finest popular book about fishes ever written. All aspects of fish natural history are covered.

Perlmutter, Alfred. 1961. "Guide to Marine Fishes." New York University Press, New York. A good, easily used key to marine fishes found from Cape Cod to Cape Hatteras. It is well illustrated and nontechnical.

Scott, W. B. 1954. "Freshwater Fishes of Eastern Canada." University of Toronto Press, Toronto, Canada. An excellent, semipopular guide for the area covered. Good illustrations.

Trautman, Milton B. 1957. "The Fishes of Ohio." Ohio State University Press, Columbus, Ohio. Although this is a state book, it is of such excellent quality it deserves mention here. Each species is discussed not only taxonomically but ecologically as well. Excellent line illustrations are included for each species.

Amphibians and Reptiles

Bishop, Sherman. 1943. "Handbook of Salamanders." Comstock Publishing Associates, a division of Cornell University Press, Ithaca, N.Y. One of the Handbooks of American Natural History series, this excellent book represents the mature work of one of the great American authorities on salamanders. It is complete, well illustrated, and authoritative, though moderately technical in some respects. Keys to all species occurring in North America north of Mexico are included.

Carr, Archie. 1952. "Handbook of Turtles." Comstock Publishing Associates, a division of Cornell University Press, Ithaca, N.Y. This attractive and well-written volume is another of the Handbooks of American Natural History series. Carr is among the most readable of present-day natural history writers as well as an authority on turtles.

Conant, Roger. 1958. "A Field Guide to Reptiles and Amphibians." Houghton Mifflin Company, Boston. An excellent and well-illustrated field guide in the Peterson series, written in a popular style, and so accurate it has been widely acclaimed by authorities.

Goin, Coleman J., and Olive B. Goin. 1962. "Introduction to Herpetology." W. H. Freeman and Company, San Francisco. A textbook on the subject, written for students with a background of a year of college biology.

Noble, G. K. 1931. "The Biology of the Amphibia." McGraw-Hill Book Company, New York. (Reprinted 1954 by Dover Publications, Inc., New York.) Long the standard reference for general information about amphibian biology, this book is again available. No serious student of amphibia should be without it.

Oliver, J. A. 1955. "Natural History of North American Amphibians and Reptiles." D. Van Nostrand Company, Inc., Princeton, N.J. For background reading and general information about these groups, this is the most comprehensive and up-to-date book available. It is one of the New Illustrated Naturalist series.

Pope, Clifford. 1939. "Turtles of the United States and Canada." Alfred A. Knopf, Inc., New York. Although supplanted somewhat by Carr's book (see above), this is still a valuable reference and is perhaps less technical than Carr.

———. 1955. "The Reptile World." Alfred A. Knopf, Inc., New York. This is a beautifully printed volume of up-to-date and pertinent information about reptiles. Pope writes in a most entertaining manner, and the information is authentic.

Schmidt, Karl, and D. D. Davis. 1941. "Field Book of Snakes of the United States and Canada." G. P. Putnam's Sons, New York. Almost a model of what a field guide should be, this little book is indispensable to the collector of snakes. The keys are usable, the illustrations good, and the information accurate.

Smith, Hobart. 1946. "Handbook of Lizards." Comstock Publishing Associates, a division of Cornell University Press, Ithaca, N.Y. This is one of the early volumes in the Handbooks of American Natural History series and one of the best. It is a compendium of information which will permit identification of lizards and will also tell the reader practically everything known about them at the time of writing. One valuable feature of this book is the inclusion, after each species or group, of a brief discussion of unsolved problems on which the interested biologist might work.

Stebbins, Robert C. 1954. "Amphibians and Reptiles of Western North America." McGraw-Hill Book Company, New York. Regional works are often of special value, and this is a good one. Western herpetologists will find it of great interest. Coverage is the United States and Canada, westward from the eastern borders of New Mexico, Colorado, Wyoming, Montana, Saskatchewan, and Mackenzie.

Wright, A. H., and A. A. Wright. 1949. "Handbook of Frogs and Toads." 3d ed. Comstock Publishing Associates, a division of Cornell University Press, Ithaca, N.Y. A massive amount of information about every aspect of the life of frogs and toads. Good keys to both larvae and adults, illustrations of the species, and range maps are all important features of this volume of the "Handbook" series.

———. 1957, 1962. "Handbook of Snakes of the United States and Canada." Vols. I, II, Comstock Publishing Associates, a division of Cornell University Press, Ithaca, N.Y. Vol. III, A. H. Wright and A. A. Wright, Ithaca, N.Y. The most recent in the "Handbook" series, by the editor and his wife. The same excellent quality and format as their frog and toad book, these volumes present complete information on American snakes. Volume III is a bibliography on snakes.

BIRDS:

Birds are undoubtedly the most popular group of vertebrates among amateur biologists, and as a result the popular literature of birds is far more extensive than that of most other groups. The list given here is only a sample, but Pettingill (1956) presents a very extensive bibliography of both popular and technical works.

Alexander, W. B. 1963. "Birds of the Ocean." 3d ed. G. P. Putnam's Sons, London. A field guide having keys within orders. The nomenclature and some facts such as ranges are out of date—really a reprint of second (1954) edition—but still an excellent manual.

Allen, A. A. 1961. "The Book of Bird Life." D. Van Nostrand Company, Inc., Princeton, N.J. This book has served as a textbook for ornithology courses, but it is also suitable for general reading. Illustrations are, for the most part, photographs by the author.

Bent, A. C. 1919 and following. "Life Histories of North American Birds." 19 vols. to date. U.S. National Museum, Washington, D.C. This monumental work, when completed, will furnish the most comprehensive reference on natural history of birds ever attempted. Earlier volumes are out of print, although several have been reprinted, and all are available at good libraries. Now being reprinted by Dover Publications, Inc., New York.

Chapman, Frank M. 1932. "Handbook of Birds of Eastern North America." 2d ed. Rev. ed. Appleton-Century-Crofts, Inc., New York. Chapman probably did more to popularize bird study than any other person. This book is semitechnical, with keys to the species and a wealth of other ornithological information. Outdated in many respects, but still useful.

Kortright, F. H. 1942. "The Ducks, Geese and Swans of North America." Wildlife Institute, Washington, D.C. Books about particular groups of birds are too numerous to be mentioned here, but this one merits inclusion as a model of its kind. The text is comprehensive and authentic, the illustrations among the best ever printed. Plates of hybrid ducks and downy young and other plumages represent a real contribution to scientific ornithology.

Palmer, Ralph S. (ed.). 1962. "Handbook of North American Birds. Vol. 1. Loons through Flamingos." Yale University Press, New Haven, Conn. The first volume of a planned set. An unusually thorough compilation of knowledge on every facet of the life history of each species.

Peterson, R. T. 1961. "A Field Guide to Western Birds." Rev. ed. Houghton Mifflin Company, Boston. The companion volume to the eastern guide listed below, this book covers the area west of the 100th meridian.

———. 1947. "A Field Guide to the Birds." 2d ed. Houghton Mifflin Company, Boston. With this field guide and a pair of binoculars, thousands of Americans have become competent in identification of birds in the field. The Peterson system of identification by quick recognition of diagnostic marks has greatly improved the level of accuracy of field students everywhere.

Pough, R. H. 1946. "Audubon Bird Guide: Eastern Land Birds." Doubleday and Company, Inc., Garden City, N.Y. (see entry following).

———. 1951. "Audubon Water Bird Guide: Water, Game and Large Land Birds." 2 vols. Doubleday and Company, Inc., Garden City, N.Y. These two companion volumes represent the entry of the Doubleday Nature Guide series in the bird book field. They feature excellent colored illustrations and considerable general information about each species. The two volumes have also been issued in a one-volume edition.

———. 1957. "Audubon Western Bird Guide: Land, Water and Game Birds." Doubleday & Company, Inc., Garden City, N.Y. Follows the same plan as the above volumes.

Saunders, A. A. 1951. "A Guide to Bird Songs." Doubleday & Company, Inc., Garden City, N.Y. The increased availability of bird-song recordings has reduced the usefulness of such books as this, but Saunders' unique system of recording and remembering songs is still of interest to field ornithologists.

Van Tyne, Josselyn, and Andrew Berger. 1959. "Fundamentals of Ornithology." John Wiley & Sons, Inc., New York. About one-third of this advanced text covers the world's bird families. The rest presents a balanced treatment of bird life.

Welty, Joel C. 1962. "The Life of Birds." W. B. Saunders Company, Philadelphia. A beginning text in ornithology with little taxonomic information but much on other aspects of bird biology.

Wolfson, Albert (ed.). 1955. "Recent Advances in Avian Biology." The University of Illinois Press, Urbana, Ill. A multi-authored survey of progress in ornithology, of great value in acquainting the student with the whole field. Some of the papers are rather technical, but there is much that is useful for the field ornithologist who is concerned with keeping up with the varied aspects of ornithological research.

MAMMALS:

Bourlière, Francis. 1956. "The Natural History of Mammals." 2d ed. Alfred A. Knopf, Inc., New York. Translated from the French original, this is one of the best general surveys of mammalogy. It is well written, easy to read, and not unduly technical.

Burt, William. 1952. "A Field Guide to the Mammals." Houghton Mifflin Company, Boston. A well-illustrated guide using the Peterson system for field identification of mammals. A handy pocket guide primarily concerned with recognition.

Cahalane, V. H. 1947. "Mammals of North America." The Macmillan Company, New York. A popular survey of American mammals, illustrated with attractive ink drawings. The author draws heavily on his extensive field experience as an employee of the National Park Service.

Cockrum, E. L. 1962. "Introduction to Mammalogy." The Ronald Press, New York. A detailed survey of the world's mammals, with chapters on the major facets of mammalian biology. Designed as a college-level text.

Davis, David E., and Frank B. Golley. 1963. "Principles in Mammalogy." Reinhold Publishing Corporation, New York. Like the above book, primarily a text, but with emphasis on ecology, populations, energy dynamics, and so forth, rather than on taxonomy.

Glass, Bryan. 1951. "A Key to the Skulls of North American Mammals." Burgess Publishing Company, Minneapolis. A technical key in most cases going only to genera. The abundant line drawings illustrate skull characteristics.

Hall, E. Raymond, and Keith R. Kelson. 1959. "The Mammals of North America." 2 vols. The Ronald Press Company, New York. A compendium of facts about each species of mammal found on this continent. A technical work but also of use to the beginner.

Hamilton, W. J., Jr. 1939. "American Mammals." McGraw-Hill Book

Company, New York. A clearly written and authentic survey of the general natural history of North American mammals. Information on prehistoric mammals is especially good. Each chapter covers a particular aspect of mammalian life, including food, reproduction, homes, classification, and so forth.

———. 1943. "The Mammals of Eastern United States." Comstock Publishing Associates, a division of Cornell University Press, Ithaca, N.Y. An excellent identification guide and general reference to the mammals of this region. Keys to families and genera and good illustrations aid in identification. Coverage of life history is especially extensive. One of the Handbooks of American Natural History series, this is indispensable for the student of mammals east of the Mississippi.

Murie, Olaus. 1954. "A Field Guide to Animal Tracks." Houghton Mifflin Company, Boston. The title does not fully indicate the tremendous amount of information included in this little volume. A good survey of the use of animal signs in interpreting natural events. One of the Peterson field-guide series.

Palmer, Ralph S. 1954. "The Mammal Guide." Doubleday & Company, Inc., Garden City, N.Y. One of the Doubleday series of nature guides, this is the most information-packed guide to mammals yet produced. The numerous colored illustrations supplement a concise text which covers the habits of mammals in an excellent manner.

Seton, E. T. 1929. "Lives of Game Animals." Doubleday & Company, Inc., Garden City, N.Y. Reprinted in 1954, this classic work is now available for a new generation of naturalists. The price of the eight beautifully illustrated volumes is beyond the range of many mammalogists, but it is an outstanding reference and an attractive addition to the naturalist's library. Pure natural history, it is based largely on Seton's own field work, which spanned more than half a century. The outstanding work of one of the last great naturalists.

SOURCES OF BIOLOGICAL LITERATURE (other than publishing houses)

Books from regular publishers are the main source of biological information for most amateur biologists. The more advanced amateurs and the professional biologists, however, are usually aware of other sources. Many of these sources publish material which is of interest to every naturalist, so we give here a brief summary of the more important publishers of such material.

FEDERAL AGENCIES: All publications of the Federal government can be purchased from the Superintendent of Documents, Washington 25, D.C. Lists of available publications are usually obtainable from the department or branch of government by which they are prepared. Agencies which publish material of interest to biologists include the U.S. Department of Agriculture, U.S. Fish and Wildlife Service (formerly the Bureau of Biological Survey and Bureau of Fisheries), U.S. Forest Service, U.S. Soil

Conservation Service, National Park Service, and the National Museum.

STATE AGENCIES: Most state governments engage in some kind of biological study of the state. The work of the agencies which perform these studies is usually published by the state and is given free or sold at cost to interested residents of the state. Among the organizations which may do state biological studies are natural history surveys, state museums, conservation departments, experiment stations, state colleges, or universities. Faunal and floral lists, popular guides to local areas, and sometimes sumptuous volumes on such groups as birds and wildflowers may be available.

MUSEUMS: Many public museums, particularly the larger ones such as those in Chicago and New York, publish a wealth of biological information. Guides to the local plants and animals are often available, and many are directed at the amateur naturalist or even at the beginner. Technical series, based on work in the collections of the museum, are often produced. A list of such publications may usually be secured by writing to the director of the museum.

PUBLIC EDUCATIONAL ORGANIZATIONS: The rise of popular nature study has led to the formation of numerous groups whose interest in nature provides a common bond. Some of these groups include in their activities publication of educational material, which is often of great value to the amateur or beginning naturalist. Among the organizations active in this field are the American Nature Association, National Audubon Society, National Wildlife Federation, Wildflower Preservation Society, Defenders of Furbearers, and the Wilderness Society.

COMMERCIAL ORGANIZATIONS: Business firms whose main sales are biological or scientific materials often publish booklets or pamphlets to aid their customers. Other business organizations sometimes publish nature-study information at the popular level for public relations purposes. Biological supply houses (see p. 440) are one of the major sources for this kind of material.

JOURNALS FOR THE FIELD BIOLOGIST

The student who wishes a reasonably complete list of the biological journals of the world may find an up-to-date list in "Biological Sciences Serial Publications, a World List, 1950–1954" by J. H. Richter and C. P. Daly, published by the Library of Congress, 1955. This publication lists about 3,500 biological serials. Shorter lists, adequate for most purposes, may be found for botany in "Taxonomy of Vascular Plants" by G. H. M. Lawrence, The Macmillan Company, New York, 1951, pp. 310–317; for zoology, in "Guide to the

Literature of the Zoological Sciences" by Roger Smith, Burgess Publishing Company, Minneapolis, 1962.

The list given here makes no pretense to completeness. It is an attempt to cover the major publications in the various branches of field biology, with special reference to those which the nonprofessional biologist may read with understanding. Only American and Canadian journals are included, since it is likely that these are the only ones available to most of our readers, and since they contain a very large proportion of the papers which would interest American field biologists.

American Fern Journal. 1910 and following. Published by the American Fern Society. This journal covers ferns and fern allies, and includes much of interest to the nonprofessional.

American Journal of Botany. 1914 and following. Published by the Botanical Society of America. One of the biggest and best technical publications in the field of botany, this journal is primarily of interest to the professional.

American Midland Naturalist. 1909 and following. Published by the University of Notre Dame, Notre Dame, Ind. Although this journal specializes in papers about the natural history of the central part of the country (hence the name *Midland*), papers on any aspect of biology are accepted. Unusually long papers are sometimes published as monographs, occupying an entire issue.

American Naturalist. 1867 and following. Journal of the American Society of Naturalists. One of the oldest biological journals in America, the *American Naturalist* is largely concerned with matters of morphology, evolution, and physiology. Occasionally papers of interest to the field student are included.

Annals of the Entomological Society of America. 1908 and following. Published by the Entomological Society of America. This is the most important entomological journal in America, particularly for taxonomic and morphological studies.

The Auk. 1884 and following. Journal of the American Ornithologists Union. One of the world's great bird journals, *The Auk* succeeded the *Bulletin of the Nuttall Ornithological Club* as the leading journal of American ornithology. Papers of general interest on the ornithology of any section of the world are included, and most of the short notes which fill the back of each issue are field notes.

Biological Bulletin. 1898 and following. Published by the Marine Biological Laboratory, Woods Hole, Mass. Coverage of this monthly journal is general, with major emphasis on marine biology.

Canadian Entomologist. 1868 and following. Journal of the Entomological Society of Canada and the Entomological Society of Ontario. This is a major entomological journal, primarily concerned with the insects of Canada.

Canadian Field-naturalist. 1887 and following. Published by the Ottawa Field-naturalist's Club. (Succeeded the *Ottawa Naturalist.*) Most of the articles in this fine journal are of interest to the field student. Papers on all phases of natural history are accepted.

The Condor. 1899 and following. Journal of the Cooper Ornithological Club. This large and valuable publication is confined to the study of birds, mostly those of the western United States.

Copeia. 1913 and following. Journal of the American Society of Ichthyologists and Herpetologists. This publication started as a loose serial but now appears quarterly. Any kind of material on fishes, amphibians, or reptiles may appear here. It is the leading American journal in this field.

Ecology. 1920 and following. Journal of the Ecological Society of America. *Ecology* is one of the great ecological journals in the world. Many of the papers are highly technical; others are of interest to the less skilled field worker.

Ecological Monographs. 1930 and following. Published by the Ecological Society of America. Papers which are too long for inclusion in *Ecology* may be published here. Any phase of ecology may be covered.

Evolution. 1947 and following. Journal of the Society for the Study of Evolution. This relatively new journal has assumed international stature. It includes papers dealing with any phase of evolution in any part of the world.

Journal of Heredity. 1910 and following. Published by the American Genetic Association. Though not concerned with field biology, this leading American genetics journal contains items of interest to all biologists.

Journal of Mammalogy. 1919 and following. Journal of the American Society of Mammalogists. This is the only journal in the English language devoted solely to the study of mammals. Coverage is world-wide, although most of the papers are concerned with North America.

Journal of Parasitology. 1914 and following. Journal of the American Society of Parasitologists. Papers on all aspects of animal parasitism appear in this bimonthly journal. It is one of the leading journals of its kind in the world.

Journal of Wildlife Management. 1937 and following. Journal of the Wildlife Society. This is an excellent quarterly publication devoted to wildlife research and management. Much good natural history material on species of economic importance is included.

Quarterly Review of Biology. 1926 and following. Although primarily a review journal, offering excellent reviews of biological books, this journal includes one or more technical papers in each issue. Some of these are interesting to the field biologist.

Rhodora. 1899 and following. Journal of the New England Botanical Club. Botany of the Northeast is covered by this small journal.

Science. 1883 and following. This is perhaps the only weekly journal of science in America. Published by the American Association for the Advancement of Science, it covers the whole field of science, so the number of papers of interest to any one biologist may not be large. Most of the papers are brief reports on discoveries or advances which may be of immediate interest to other workers.

BIBLIOGRAPHIES

Bay, J. C. 1910. "Bibliographies of Botany." *Progressus Rei Botanicae,* 3:331–456. Although now out of date, this work is valuable for the student who wishes information about publications of the eighteenth and nineteenth centuries.

Bibliography of Agriculture. 1942 and following. U.S. Department of Agriculture, Washington. Published monthly, this valuable reference covers a wide variety of biological subjects. It is particularly useful for its coverage of publications of state experiment stations.

Biological Abstracts. 1926 and following. Philadelphia, Pa. The most comprehensive and widely used biological abstracting journal in the country, and probably in the world, this is one of the primary references for the biologist. The inclusion of an abstract (brief summary) of the papers listed is a valuable feature.

Blake, S. F., and Alice C. Atwood. 1942. "Geographical Guide to Floras of the World." Part I, U.S. Department of Agriculture Misc. no. 401. This publication covers Africa, Australia, the Americas, and the islands of the Pacific, Indian, and Atlantic Oceans. Part 2 has not yet been published. In addition to the list of floras, suggestions are given as to the construction of a floral list. Even though incomplete, it is the most useful guide of its kind, and is indispensable to the botanist.

Botanical Abstracts. 1918–1926. Baltimore, Md. This publication was superseded by *Biological Abstracts*, so that its life was relatively short. It is useful for the period which it covers.

Dayton, William. 1952. "United States Tree Books: A Bibliography of Tree Identification." U.S. Department of Agriculture Bibliographical Bulletin 20. The student who needs a local publication on trees may find here a list of those available.

Dean, Bashford. 1916–1923. "Bibliography of Fishes." 3 vols. More than 35,000 references are covered in this great classic of biological bibliographies. It is now badly out of date but still extremely valuable for the period it covers.

Index Londinensis to Illustrations of Flowering Plants, Ferns, and Fern Allies. 1920–1931, with supplement, 1941. Oxford University Press, London. This tremendous publication lists the place of publication of illustrations of plants in the groups listed. The years from 1753 to 1935 are covered. For the student who wishes to see a picture of a particular plant, particularly one which has not been shown in many publications, this is a helpful work to have at hand. It may be found in most libraries where botanical research is done.

Index to the Literature of Economic Entomology. 1890 and following. This entomological index, indispensable to the worker in that field, was begun under the Department of Agriculture, and has been sponsored in recent years by the American Association of Economic Entomologists. Because it was for many years prepared by Mabel Colcord, it has become known as the Colcord Index. Numbers appear at three- to five-year intervals. Coverage includes North America and the West Indies, in varying degrees of completeness.

International Catalog of Scientific Literature. 1902–1919. Royal Society, London. This short-lived catalogue is useful for the short period during which it contained biological material, but it is not one of the primary references.

Jackson, B. D. 1881. "Guide to the Literature of Botany." Longmans, Green & Co., Ltd., London. Although very much out of date, this large volume is often useful for literature of the nineteenth century.

Rehder, A. 1911–1918. "The Bradley Bibliography: A Guide to the Literature of the Woody Plants of the World Published Before the Beginning of the Twentieth Century." 5 vols. Harvard University Press, Cambridge, Mass. The title of this work indicates its coverage and value.

Smith, Roger C. 1962. "Guide to the Literature of the Zoological Sciences." 6th ed. Burgess Publishing Company, Minneapolis. For the beginner, adventuring into the field of biological literature, this book is a necessity. For the more advanced student, it is an almost indispensable reference. Although confined to zoological literature, it contains many publications which cover the whole field of biology and also presents valuable information about conducting a literature search, writing a scientific paper, and other matters of interest to the biologist. This is one of the most valuable and least expensive of bibliographic aids.

Strong, R. M. 1939–1946. "A Bibliography of Birds." 3 vols. Field Museum of Natural History, Zoological Sciences Bulletin 25. Chicago, Ill. The indispensable bibliography for ornithologists; tightly packed with references to the literature about birds.

Ulrich, Carolyn F. 1951. "Ulrich's Periodicals Directory." 6th ed. R. R. Bowker Company, New York. An annotated list of some ten thousand world periodicals, with information about the content of each one.

Union List of Serials. 1943 and following. The H. W. Wilson Company, New York. This is one of the most valuable publications for the scientist. It lists the holdings of serials in American libraries, so that the worker who wishes to consult a particular publication can readily discover where it is obtainable.

United States Book Catalog and the Cumulative Book Index. 1928 and following. The H. W. Wilson Company, New York. A cumulative list of books published and available in the United States, of particular value in determining date of publication and other information about books.

Wildlife Abstracts. 1952 and at irregular intervals following. The items cited in *Wildlife Review* (see below) are periodically gathered into a summary volume. The three volumes thus far published cover 1935–1951, 1952–1955 and 1956–1959.

Wildlife Review. 1935 and following. U.S. Fish and Wildlife Service, Washington. For workers in the field of wildlife management, this publication is a necessity. For other biologists, it is a very valuable tool. Its coverage is wider than the title would imply, and each article is briefly reviewed. It appears irregularly, about four times each year.

Wood, C. A. 1931. "An Introduction to the Literature of Vertebrate Zoology." Oxford University Press, London. Although now out of print, this book is available in many good libraries and is of great value as an introduction to the field.

Zoological Record. 1864 and following. Zoological Society of London. The number-one reference for the zoologist. The length of time cov-

ered, and its inclusion of references from the whole world, make this bibliography essential to any literature survey.

SOME TOOLS AND TECHNIQUES OF THE FIELD BIOLOGIST

The observations of the old-time field biologist were made with the unaided senses or with simple instruments. Modern ecology, with its insistence upon precise data, has become more dependent upon instrumentation; and the recent development of miniaturized electronic instruments, improved optical equipment, and many other new tools have literally revolutionized field study. Calculations which could once be performed only laboriously in the laboratory are now made by automatic instruments in the field.

A simple listing of available instruments would require more space than we can give to this subject. Our aim is not to give a comprehensive list but to indicate a few of the major instruments and tools, briefly discuss a few techniques, and point out to the student sources for more detailed information in each of the areas discussed.

Optical Supplies and Instruments

MICROSCOPES: One of the basic tools of the biologist, the microscope, is unfortunately expensive. Ordinary microscopes of high quality cost from $500 to $1,500, while such special types as phase-contrast microscopes are even higher priced. The small microscopes which sell for $5 to $50 in hobby stores are limited by the very small size of field and the very poor illumination, even if the optical quality is adequate. A used microscope is the best that an impecunious amateur can hope for, and it should be chosen with great care from a reputable company and with a guarantee, if possible.

For much of the field work involved, a low-power dissecting microscope which has magnification of 5 to 30×, or more with different lenses, is the desired instrument. This is less expensive than a compound microscope but is, of course, virtually useless for studying genuinely microscopic objects such as Protozoa.

American manufacturers of microscopes include American Optical Company and Bausch and Lomb Optical Company. European microscopes include the Leitz, Zeiss, and Wild, all marketed in this country. In addition, there are several lines of Japanese-made microscopes, some of which are optically and mechanically satisfactory and which are generally relatively low in price. The prospective buyer should contact the suppliers of biological equipment listed on p. 461 for information about such equipment.

BINOCULARS: Most field biologists require binoculars, although they are particularly essential for ornithologists. A good prism binocular of 6 to 8 power is essential. In general, the diameter of the objective lens should be five times the magnification; thus the glass will be described as a 6 x 30, 7 x 35, or 8 x 40. For greatest versatility, the 7 x 50 is preferred because of its very high degree of light transmission. Higher powers of 10 to 16 power generally require a tripod.

Binoculars should be checked by a competent operator before purchase for: *alignment*—divergence of one of the oculars from precisely the same field as the other; poor alignment will cause distortion and eyestrain; *chromatic aberration*—a fault which produces rainbows around observed objects and is the result of poor optical quality; *general construction*—seating of lenses, fineness of mechanical finish, attachment of prisms, and so forth. In short, binoculars should be purchased only from a trustworthy supplier and only with a guarantee.

Binoculars are made by most of the same firms which make microscopes. Advertisements may be found in ornithological and nature publications such as *Audubon Magazine*.

TELESCOPES: The most popular telescopes for field use are the 20-power "spotting scopes" which are seen in the hands of bird watchers on any field trip. Many of these have interchangeable lenses which permit magnifications up to 60 power. In general, the greater the power, the smaller the field of view, but 20 to 60 power covers the usual range of use. The development of new catadioptric telescopes with much higher magnifications has added a new (though expensive) tool to the optical equipment of the field biologist. The best known of these is the Questar, which is only about eight inches long but has higher magnification than the larger type of scope. These instruments, like many telescopes, can be attached to a camera for super-telephoto photography.

HAND LENSES: The hand lens is the mark of the botanist, as the binoculars are of the ornithologist. Good hand lenses may be secured from biological supply houses for $5 to $15. They have magnification up to 20×, but 10× is the most common power.

CAMERAS: Inevitably, every field biologist will wish to use a camera to record events or scenes connected with his field work. The number of different makes and models is staggering, but they may be divided into a relatively few major types, within which price and refinements are the major differences. Four types are most commonly used in field study, and we shall consider only these types.

1. THE SINGLE-LENS REFLEX CAMERA. These cameras have been in use for many years, with the old Graflex being the prototype. This was a large camera, taking cut film in sizes up to 4 by 5 inches (or even larger in some cameras). Many are still in use, and early

nature photographers used them extensively. Currently, this same type of camera, in which a mirror behind the lens focuses the image on the ground glass or through a prism, is most popular in the 35-mm or 2¼- by 2¼-inch format. Such a camera is ideal for close-up work, since the viewer sees almost precisely the same field as the lens covers. These cameras are also very versatile, and most kinds feature a variety of telephoto lenses, bellows extensions for close-ups, and other accessories. Most models cost from $100 to $300, although there are a few both above and below that range. Probably more biologists use this type of camera than any other.

2. THE RANGE-FINDER CAMERA. This type was made popular by the excellent Leica, Contax, Nikon, and others which were the favored cameras of the 1930s and 1940s. Most are 35-mm, but the small negative size is partially offset by the excellence of the lenses and by the quality of modern films. An almost unlimited variety of accessories is available for the more expensive types, but cameras of this type may be priced from $50 to $500. With the proper accessories, the range-finder camera is as versatile as the single-lens reflex and is preferred by many biologists.

3. THE TWIN-LENS REFLEX. The prototype of this camera type is the Rolleiflex, which is still one of the most popular cameras made. Most such cameras are 2¼ by 2¼ inches in format, though a few are available in other sizes. They are sturdy, fast, and convenient, and the negative size is adequate for sizable enlargements. The problem of parallax arises at close range, i.e., the viewing lens does not cover precisely the same field as the taking lens, but the better models have close-up attachments which overcome this shortcoming. Prices range from about $30 to $300.

4. THE VIEW CAMERA AND PRESS CAMERA. Although these are two quite distinct types, they are treated together because they have somewhat similar characteristics. In general, the view camera is designed for use only on a tripod and primarily in a studio, while the press camera is more portable and is designed to be used handheld. These cameras have the advantages of extreme versatility and large negative size (2¼ by 3¼ inches to 8 by 10 inches), but are relatively bulky, and the accessories and plateholders are also large. Some biologists insist that the quality of the photograph makes up for the added weight and bulk, but this argument has lost some of its validity with the development of modern fine-grained films. Where large negatives are required, however, these are the cameras to choose.

Camera Accessories: The more expensive cameras have an impressive array of accessories for every purpose. Some of those of special interest to biologists are:

1. Telephoto lenses. These lenses serve the same function for the camera that the binoculars do for the eye. They are available in all lengths, and in varying degrees of refinement. The magnification of a telephoto lens is equal to its focal length divided by the focal length of the normal lens of the camera. Thus a 200-mm lens would magnify four times as much as the normal 50-mm lens on a 35-mm camera.

One of the problems for the camera user is what telephoto lenses to purchase. Generally the 135-mm is considered first choice for the 35-mm camera owner. Second choice would be a longer lens, perhaps 300- or 400-mm for bird photography or any other long-distance use. An inexpensive substitute is a device which permits the use of binoculars as telephoto lens. Even telescopes may be used with a suitable attachment.

A recent addition to the field of photography is the use of a modified Barlow lens behind a lens, to virtually double its focal length. Thus a 135-mm telephoto with this added accessory, becomes about a 250-mm lens. These attachments are quite inexpensive, and are a boon to the camera owner who cannot afford numerous telephoto lenses.

2. Close-up accessories. The normal camera lens will focus no closer than 1½ to 3 feet. Since many biologists wish to photograph very small objects, several devices have been produced to make this possible. The cheapest are the close-up lenses, which can be used on virtually any camera and cost only a few dollars. For single-lens reflex cameras, the normal lens is used with the addition of extension tubes or a bellows, which puts the lens farther from the film and permits extreme close-up work. With press and view cameras, the bellows may be racked out to achieve the same result.

3. *Wide-angle lenses.* The field biologist working in the wide-open spaces seldom needs a lens which will permit him to include in the picture a wider field. Sometimes, however, such an accessory is essential, and since they are not expensive (except for very fast and very high quality lenses) the well-equipped photographer should have one in his kit.

4. Filters. Filters are inexpensive pieces of glass or plastic, tinted to filter out certain colors and thus modify the image as it will appear on the film. Red and yellow filters are most often used in black-and-white photography to darken the sky and make clouds stand out. Filters for color film are designed to make up for changes in the color temperature of the light under different conditions. Experience will tell the photographer which filters he frequently needs, and they are so inexpensive that one may own a variety of different kinds.

5. Film. Perhaps film may not be properly considered an accessory, but it is an important aspect of picture quality. Films today, both color and black-and-white, are better than ever. Probably personal preference is the only guide until you have tried different kinds, but our preference in black-and-white is: for all-purpose work, Kodak Plus-X or Perutz Peromnia 21; for extremely fine-grained work, Kodak Panatomic-X or Adox KB 14. For extremely fast film, under poor light conditions, Kodak Improved Tri-X or Ansco Super-Hypan. No doubt many photographers would disagree with our choices, but the above films are generally available, and all are of excellent quality. For color work, Kodachrome II is the standard of excellence against which others are measured. Among high-speed color films, both Kodak and Ansco have excellent products. If prints are the major aim, rather than transparencies, Kodacolor may be the best choice.

6. Polaroid equipment. "Picture-in-a-moment" equipment rates a separate section. For the biologist, perhaps its greatest value is as a kind of test view—a means of seeing what a picture will look like before taking it on regular negative film. For some cameras, Polaroid negative film is available, and the recent addition of Polacolor makes it a more versatile system. There are some limits to its versatility, but Polaroid remains one of the most exciting advances in photography and a system with many uses for the biologist.

Instruments for Measuring Environmental Conditions

The environment of an organism is made up of biological and physical components. We have discussed the study of the first in some detail. Study of the physical environment is largely a matter of instrumentation, and a few of the most important instruments will be discussed here.

INSTRUMENTS FOR MEASURING ATMOSPHERIC CONDITIONS

1. Light. Light measurements are generally made with a photoelectric meter, either one such as is used for photography or one specially constructed for ecological work. These instruments measure light intensity in foot candles by means of a photoelectric cell. Recent development of cadmium-sulphide meters provides greater sensitivity.

2. Temperature. For most field measurements, a properly calibrated mercury thermometer is adequate. When variation in temperature is important, a maximum-minimum thermometer may be left in place and checked daily. For continuous recording, a thermograph will record temperatures on a paper attached to a revolving drum.

For many purposes, however, neither the standard thermometer nor the thermograph is suitable. Electronic thermometers, using the thermistor principle, may be used in almost any kind of location; with a variety of probes the same instrument may serve for subsoil measurements or for checking blood temperature of small animals. Battery-operated models which will record temperatures from −15 to 50° Centigrade are available at less than $100 and will cover the ordinary range of environmental temperatures.

Potentiometers, which make use of thermocouples and which also have many types of probes, are much used in ecological work. These may require a conversion table so that the millivolt readings can be converted to temperatures, thus being less convenient than electronic thermometers.

3. Evaporation and transpiration rates. The Livingston atmometer, widely used in the determination of evaporation rate, is a porous clay sphere attached to a water container. When water evaporates from the sphere, it is replaced by water drawn up from the container, and decrease of water in the container is a measure of the rate of evaporation.

Transpiration is often measured by the use of paper treated with cobalt chloride. When dry, the paper is blue. As it takes up moisture, it changes to pink. A piece of the paper is attached to a leaf between glass plates. The time required for the paper to turn completely pink is a relative measure of the transpiration rate.

4. Relative humidity. Two types of psychrometers are used in measuring relative humidity. The sling psychrometer has a dry-bulb thermometer and a wet-bulb thermometer attached to a handle by which they may be whirled through the air. Evaporation of water from the wet bulb lowers the temperature recorded by that thermometer, and the difference between that temperature and the temperature recorded by the dry bulb thermometer is a measure of relative humidity. Standard tables are used to convert the readings.

The cog psychrometer is a sort of modified eggbeater, which can be used in spaces too confined for whirling the sling psychrometer. A handle is turned which revolves the two thermometers, producing the result described above.

The dew-point apparatus operates on a different principle. A rubber bulb is attached to a silver-lined vessel which contains: *a*, ether, *b*, an open-end glass tube through which the air escapes, and *c*, a thermometer. Evaporation of the ether lowers the temperature of the metal as air is forced through, and when it reaches a certain temperature, dew condenses on the outside. Since the dew point depends upon the humidity, conversion tables can be used to convert the dew-point temperature into a relative-humidity reading.

Direct-reading instruments to measure humidity are also available, but these are more expensive than the traditional instruments described above. For long-term observations, instruments for recording humidity can be used.

5. Wind. Movement of air in open areas is measured by an ordinary anemometer. In more confined areas, a katathermometer is used. This instrument operates on the principle that movement of air increases evaporation of a column of alcohol, thus lowering the temperature. The temperature can thus be converted into a measure of air movement.

INSTRUMENTS FOR MEASURING SOIL CONDITIONS

1. Temperature. See discussion of temperature above, p. 448.

2. Moisture. Moisture content of a soil can be determined by weighing out 100 grams of soil, drying it in an oven, and reweighing it. The weight loss will be the percentage of moisture in the sample. A simpler method is the soil point, a porous porcelain cone of standard size and porosity. When placed in the soil, the cone will absorb an amount of water relative to the water content of the soil and is then weighed to determine the amount absorbed.

3. Aeration. The air space in the soil may be roughly determined by calculating the amount of water the soil will hold at saturation, since water will seep into the air spaces. Although not precise, this method is usually accurate enough for ecological studies.

4. pH. For general field studies, various indicator methods are used. Colored papers change color and are then compared with a standard to determine the indicated pH. Soil-test kits contain liquid indicators which are easy to use in the field. For precise work, or when it is necessary to record pH repeatedly or over a long period, a pH meter is used. These expensive and delicate instruments must be calibrated with a solution of known pH, but they give very precise measurements.

5. Structure. Particle size is most often determined by sifting the soil through a series of sieves with successively smaller mesh. Sometimes a small sample is examined under a microscope, and the number of particles of different sizes is recorded. Organic matter content may be determined by burning off the humus in a muffle furnace, which heats the soil to a very high temperature. Nonorganic matter remains, and the amount of organic matter lost is determined by before-and-after weighing.

6. Soil profile. The depth of the various soil layers is an important aspect of its character. These may be observed and measured by digging a trench to expose the soil to the necessary depth, or more rapidly by taking a core sample with a soil auger or core sampler. One of the important uses of the core sampler is in the study of palynology (fossil pollen studies). A special core sampler can be forced into a bog to a chosen depth and then opened, driven further to secure a core and then closed, and withdrawn with an unpolluted sample from the desired depth.

INSTRUMENTS FOR MEASURING AQUATIC CONDITIONS

1. Light. The Secchi disk is a black and white disk 20 cm. in diameter. It is let down into the water on a rope or wire, and the depth at which it disappears from view is noted. Then it is drawn up, and the depth at which it reappears is noted. The average of these two figures gives a relative figure of light penetration. For more precise data on the actual amount of light at any depth, recording photometers can be used.

2. Temperature. Electrical devices are available which will record temperature at any depth by means of thermistors and a meter. The same instruments mentioned above under atmospheric conditions may be used in water with a long cable. A simpler device is the reversing thermometer. A thermometer is lowered on a wire to the depth at which temperature is to be measured. Then a metal messenger is sent down the wire to release a catch which quickly inverts the thermometer. This sudden reversal causes some of the mercury to leave the main reservoir and enter a subsidiary reservoir. The thermometer can then be raised to the surface and read. The amount of mercury which has left the main reservoir is correlated with the temperature at the point of reversal.

3. Bottom type. Dredges are used to draw up samples from the surface of the bottom. If deeper samples are needed, a core sampler is used similar to those mentioned under soil sampling above.

4. Water movement. The simplest method of measuring stream velocity is with a floating object which is timed over a measured course. This, of course, measures only the speed at the surface, and the velocity is decreased at the edges and bottom of a stream because of friction. For most purposes, however, this method is adequate.

5. Chemical conditions. Several chemical factors are important in the study of fresh-water communities. These include pH which may be determined by the methods mentioned above, oxygen content, free carbon dioxide, content of carbonates, bicarbonates, dead

organic matter, and so forth. The details of the determination of these chemicals are beyond the scope of this book, but Welch (1948) gives detailed information.

TERRESTRIAL ECOLOGICAL TECHNIQUES

1. Indicators. Certain species are so closely correlated with a certain type of community that they are termed indicators. For example, the red-backed salamander is closely linked with forests of beech and maple. The value of these indicators is limited, since they may occasionally occur in unexpected habitats, but the presence of several indicator species is often helpful in a brief determination of the general type of community.

2. Sampling methods. In any study, the entire habitat is too large for complete study. The biologist must select sample areas for study which are both random and adequate (see p. 305). In plant studies, a common method is the use of square plots called *quadrats*. In a detailed study, 25 to 50 quadrats may be chosen for detailed analysis, and the data then extrapolated to cover the whole area being studied. In a grass community, quadrats may be 1 meter square; in shrub or tree community, they are more likely to be 5 or 10 meters square. Small animals such as insects and soil invertebrates may also be studied by the examination of sample quadrats.

In forestry, in wildlife studies, and for some other uses, transects, lines through the habitat at measured intervals, are used instead of quadrats. Transects are often used when only the trees or some animal, which can be easily observed at some distance are to be counted. For example, this technique is widely used for game birds which will flush at some distance.

For larger animals, some method of sampling which will involve actual collecting is usually used. Traps of various kinds are used for most mammals. Birds, of course, are more easily observed and counted either by sight or by sound. More secretive or nocturnal forms may be counted by signs such as tracks and droppings. Several portable photographic recorders have been devised (see for example Taylor and Jean, 1964), which may be left in place and will record any animal which passes in front of the camera.

In some cases, predators are more effective samplers than the biologist. Thus the presence and relative numbers of prey species may be determined by analysis of owl pellets, predator stomachs, droppings, or remains around dens.

AQUATIC ECOLOGICAL TECHNIQUES

1. Sampling methods. In aquatic situations, the same major problems of sampling arise but are made more difficult by the

fact that the worker often cannot see the area or the organisms he wants to sample. Thus a plankton sample may be taken by drawing samples of water at specific locations and counting or otherwise calculating the captured organisms. Or a plankton net may be drawn through the water for a standard distance and the concentrated plankton sample analyzed.

Larger animals and plants may be counted in much the same way as on land, if they are readily visible. Thus a square-foot sampler may be placed on the bottom and the macroscopic organisms within it counted. Animals large enough to be marked may be censused by the Lincoln-Peterson index (see p. 307).

More detailed information on both the instruments and the methods used in ecological study may be found in the references listed below and in the books on techniques on pp. 457 to 459.

SUGGESTED READING

Bailey, A. M. 1951. "Nature Photography with Miniature Cameras." Denver Museum of Natural History, Museum Pictorial no. 1, Denver, Colo.

Kinne, Russ. 1962. "The Complete Book of Nature Photography." A. S. Barnes and Co., Inc., New York.

Oosting, Henry J. 1956. "The Study of Plant Communities." 2d ed. W. H. Freeman and Co., San Francisco.

Shumway, Herbert D. 1956. "Nature Photography Guide." Greenberg: Publisher, Inc., New York.

Taylor, J. Mary, and Henri Jean. 1964. Rechargeable battery power for a portable photographic recorder. *J. Wildlife Management,* 28:406–408.

Welch, Paul S. 1952. "Limnology." 2d ed. McGraw-Hill Book Company, New York.

———. 1948. "Limnological Methods." McGraw-Hill Book Company, Blakiston Division, New York.

Yeates, G. K. 1946. "Bird Photography." Faber & Faber, Ltd., London.

THE USE OF STATISTICS IN BIOLOGICAL STUDIES

In the study of natural history, many observations are made which are not subject to experimental proof. Science, however, demands that we be as certain as possible of our facts, and in recent years many workers have come to depend upon statistics to provide evidence. This trend has been called by some a fad, but there can be no doubt that statistical analysis of data is an extremely valuable tool in many studies. The biologist with little mathematical training must know when his work requires the use of statistics, and he must know enough about the subject to read with understanding the work of his colleagues. The more abstruse elements of statistics may well be left to competent mathematicians, and these facts are in any case too lengthy to be included here. This brief summary is intended to indicate some of the field projects in which statistical analysis is needed, as well as some of the more important methods which are used. The interested reader may further his knowledge by consulting the references which are listed at the end of this section.

Statistical analysis is restricted to data which can be expressed in numerical terms. Such data are said to be *quantitative* or *meristic*. Thus the number of feathers on the bodies of members of a particular species of bird can, if one has the patience, be counted, producing meristic data which can be statistically analyzed. The numerous instruments available to the biologist today make meristic or quantitative data obtainable in a great number of biological studies.

The basis of statistical analysis is the population which is being analyzed. This may be the trees in a forest, the animals in a field, the organisms which belong to a particular species, or any other discrete population. (It should be noted here that this is not the same usage of the word "population" as in Chap. 9.)

It is rarely possible to study an entire population. If you could do so, you would know that your facts were absolutely reliable and covered the entire range of variation within that population. Since we cannot study the whole group, we usually depend upon samples. Some of the difficulties and problems of sampling are discussed in Chap. 9. An adequate sample must be chosen in a random manner and must be large enough to include most of the range of variation of the characteristics which we are going to measure. Complete randomness would require that every member of the population had as much chance of being included in the sample as any other member. This is, of course, very difficult to achieve, but the biologist should make every effort to approach it as closely as possible.

From our sample, we derive data about the specimens included in it, and from these data we want to derive other data about the population as a whole. The most commonly derived statistics are the *range*, the *mean*, the *mode*, the *median*, and the *standard deviation*.

The *range* includes all the integers in a sample, from the smallest measurement to the greatest; it reflects the variability of the characteristic being studied.

The *mean* is the arithmetic average of the counts or measurements, derived by adding all the measurements together and dividing by the number of specimens in the sample.

The *mode* is the count or measurement which occurs most frequently in a given sample; it may or may not be close to the mean.

The *median* is the exact middle score of the distribution, and this too may or may not closely approximate the mean.

The *standard deviation* is a measure of the variation from the mean of individuals in the sample. It is usually represented by the symbol σ. In a given population, about 67 per cent of all individuals will fall within one standard deviation on either side of the mean, 95 per cent within two deviations, and 99 per cent within three deviations. The expected range of the population can thus be calculated from this statistic. It can be calculated in any of several ways, one of which can be chosen from a standard statistics text.

After the sample is taken, it is usually divided into groups or *classes* on the basis of the meristic character being used. If we were drawing a sample to determine the average height of the American male, we might use classes for every inch from 5 feet to 7 feet, with a single class for those above and below these figures. The divisions into which individuals are placed are called *class intervals*. This *frequency distribution* of your sample may be presented in the form of a graph of some kind, and in many cases this presents all the information needed.

When a characteristic is distributed at random throughout a population, a graph of its occurrence would take the form of a *normal curve*. This term has a precise mathematical definition, but for our purposes it is sufficient to say that the curve is bell-shaped, with the highest point at the middle, and curving off in the same manner in both directions, so that the mean, the mode, and the median are all at the same central high point. To return to our study of the height of American men, if we had a very large sample we might expect to get a normal curve.

If, on the other hand, we plotted the height of Americans without regard to sex, we might expect a curve with two high points, one representing the majority of males, the other representing the majority of females. This is a *bimodal curve*. When such a curve shows up, we suspect that we are dealing with two different populations, at least with regard to the characteristic studied.

If we plotted the age of American men on a graph, the high point would probably be nearer the left side of the graph, and the tail at the right end would be longer and more gradual than that at the left end. This is a *skewed curve* and indicates that the characteristic is not randomly distributed.

Frequency distributions are often used to derive other data. One common use is that of comparing two or more populations with regard to meristic characteristics. Two groups in which the ranges of the counts or measurements do not overlap would probably be regarded as two distinct species. If the ranges are essentially similar, the two samples were no doubt drawn from the same natural population. When the ranges differ in a marked way, but still overlap, we are faced with the problem of deciding whether the data indicate that the populations are different, or that individual variation can account for the differences. By applying certain statistical tests to the data, we can show that our hypothesis is either probably right or probably wrong, and can state mathematically the degree of probability. A simple example may help to explain this.

Suppose that the wing measurements of a sample of 50 birds of a species which occurs in New England range from 70 to 90 mm with a mean of 81. A similar sample from Newfoundland shows a range from 76 to 98, with a mean of 87. Obviously there is a difference, but is it statistically significant? Or, in other words, is it probable that the two samples could not have been drawn from a single homogeneous population?

There are several ways of arriving at this information, and they are too complex to be treated in detail here. The results are usually expressed in terms of percentage; e.g., the results are said to be significant at the 95 or 99 per cent level. At the 95 per cent level, this means that the odds are 95 to 5—or 19 to 1—that the hypothesis is correct; although this is not proof, it is strong evidence.

The many uses of statistics in biological research are too varied and complex to consider here. Perhaps the best way to introduce the student to such uses is to indicate some studies in which statistics have played a part, and which will serve to demonstrate some of the methods commonly used and some of the types of research which profit by statistical treatment. The papers listed in the Suggested Reading which present a cross section of biological statistics are marked (S).

These studies vary a great deal in the complexity of the statistics employed, some being very simple and some rather complicated. Simple statistics, such as graphs and frequency distributions, are used in a large percentage of biological studies. The more complex statistical operations are used less often, but in ecology and taxonomy particularly they have become important. For the biologist who has some doubts as to the needs of a particular study, it would be wise to consult a statistician before the experiments are set up. Often experiments can be designed to give satisfactory results from the statistical viewpoint, whereas if a statistician were consulted after the performance of the experiments, he might find that they were not set up to yield data suitable for statistical analysis.

SUGGESTED READING

Bartholomew, George A., Jr., and William R. Dawson. 1954. Temperature regulation in young pelicans, herons, and gulls. *Ecology*, 35:466–472. Certain physiological and morphological data are subject to statistical analysis. This paper uses statistics in analyzing the development of temperature regulation. (S)

Cazier, M. A., and A. Bacon. 1949. Introduction to quantitative systematics. *Bull. Am. Museum Nat. Hist.*, 93:347–388.

Hayne, Don W. 1950. Apparent home range of *Microtus* in relation to distance between traps. *J. Mammal.*, 31:26–39. A statistical study of the determination of home range. (S)

Kempthorne, O., et al. 1954. "Statistics and Mathematics in Biology." Iowa State College Press, Ames, Iowa.

MacLulich, D. A. 1951. A new technique of animal census, with examples. *J. Mammal.*, 32:318–328. A statistical approach to the counting problem. (S)

Mather, K. 1947. "Statistical Analysis in Biology." Interscience Publishers, Inc., New York.

Moore, P. G. 1954. Spacing in plant populations. *Ecology*, 35:222–227. The use of statistics in vegetational analysis. (S)

Rand, A. L., and M. A. Traylor. 1951. Variation in *Dumetella carolinensis*. *The Auk*, 66:25–28. Analysis of differences among members of a single species over its entire range. (S)

Wohlschlag, Donald E. 1954. Mortality rates of whitefish in an arctic lake. *Ecology*, 35:388–396. Management of wildlife is dependent upon knowledge of all phases of life history. Statistics can often be employed to advantage in securing information of this type. (S)

See also references to books on statistics at the end of Chaps. 9 and 13.

BOOKS ON NATURE-STUDY ACTIVITIES AND TECHNIQUES

Anderson, R. M. 1948. "Methods of Collecting and Preserving Vertebrate Animals." National Museum of Canada, Bulletin 69, Ottawa. Although designed for the professional biologist, this book contains a wealth of information for the person who has occasion to preserve vertebrate specimens of any kind. Furthermore, the information on where and how to capture animals is of value to those who want live animals for study.

Benton, Allen H., and William E. Werner, Jr. 1965. "Manual of Field Biology and Ecology." Burgess Publishing Company, Minneapolis. A book of techniques on the varied aspects of field biology; intended as a companion volume to the textbook by the same authors.

Cockrum, E. L. 1962. "Laboratory and Field Manual for Introduction to Mammalogy." The Ronald Press Company, New York. Second ed. This handbook includes information on field techniques, keeping a notebook, and field problems, as well as keys to mammals and other information of interest to the amateur and the professional mammalogist, too. It is designed to accompany the author's text in a college mammalogy course.

Corrington, Julian. 1957. "Exploring with Your Microscope." McGraw-Hill Book Company, New York. A semitechnical guide to the use of the microscope, not encyclopedic but authentic.

Gray, Peter. 1964. "Handbook of Basic Microtechnique." 3d ed. McGraw-Hill Book Company, New York. Somewhat more technical and detailed than the preceding book. One of the standard texts on this subject.

Headstrom, Richard. 1949. "Birds' Nests: A Field Guide." Ives-Washburn, Inc., New York (see entry following).

———. 1951. "Birds' Nests of the West: A Field Guide." Ives-Washburn, Inc., New York. These two volumes give information on nest finding and nest identification at the popular level.

Hickey, J. J. 1953. "A Guide to Bird Watching." Garden City Books, New York. There are many volumes which tell the bird watcher how to go about his hobby. This is one of the best, giving a wealth of information about tools and techniques for the field study of birds.

Hillcourt, William. 1961. "Field Book of Nature Activities and Conservation." G. P. Putnam's Sons, New York. A gold mine of facts for the amateur naturalist. Gives ideas on what to do, how to do it, and what tools you need for the study of almost any aspect of nature.

McKenny, Margaret. 1947. "Birds in the Garden and How to Attract Them." The University of Minnesota Press, Minneapolis. The easy way to study birds is to attract them to your property as residents or as guests. This handsome book will explain the techniques of attracting by such easy means as feeding trays or such major operations as landscaping the home grounds.

Miller, David F., and Glenn W. Blaydes. 1962. "Methods and Materials for Teaching the Biological Sciences." 2d ed. McGraw-Hill Book Company, New York. The first part is concerned with teaching methods in science and is thus of interest only to teachers. Most of the book, however, is a gold mine of information about techniques, collecting, and other aspects of biology, much of which is of value in field work.

Moore, Clifford. 1954. "Book of Wild Pets." G. P. Putnam's Sons, New York. Whether you are keeping a pet or maintaining captive animals for study, this book gives information about the requirements of all kinds of wild animals in captivity, which will help you keep your animals alive, healthy, and comfortable.

Murie, Olaus. 1954. "A Field Guide to Animal Tracks." Houghton Mifflin Company, Boston. See review under the list of books about mammals.

Needham, J. G. (ed.). 1937. "Culture Methods for Invertebrate Animals." Comstock Publishing Associates, a division of Cornell University Press, Ithaca, N.Y. A compendium of techniques, this book draws on the experience of hundreds of biologists. It would be difficult to name an invertebrate group which is not included. Reprint edition now available from Dover Publications, Inc., New York.

Peterson, A. M. 1953. "A Manual of Entomological Techniques." 7th ed. Published by the author, Ohio State University, Columbus, Ohio. Every phase of entomological technique is covered in this book. Information on collecting, rearing, experimental setups, and many other aspects of entomological work is given, with abundant illustrations of the necessary equipment.

Pettingill, O. S., Jr. 1956. "A Laboratory and Field Manual of Ornithology." 3d ed. Burgess Publishing Company, Minneapolis, Minn. Although designed for use in ornithology courses, this large and handsome volume is a worthy addition to the library of any student of birds. The bibliography is one of the most useful features of the book.

Oldroyd, H. 1958. "Collecting, Preserving and Studying Insects." The Macmillan Company, New York. A good guide for the beginner in entomology.

Pray, Leon. 1943. "Taxidermy." The Macmillan Company, New York.

Though small, this book gives an adequate introduction to the subject. It is well illustrated and simply written, so that even the younger naturalist will find it useful.

Rounsefell, G. A., and W. H. Everhart. 1953. "Fishery Science: Its Methods and Applications." John Wiley & Sons, Inc., New York. Designed for the professional worker in fish management, this book contains so much information about techniques in fish study that it is valuable to any naturalist.

Smithsonian Institution. 1944. "A Field Collector's Manual in Natural History." Smithsonian Institution, Publ. no. 3766. Designed for the field workers of the Smithsonian Institution, this book contains a wealth of valuable information for the field biologist.

Wagstaffe, R. J., and J. H. Fidler. 1955. "The Preservation of Natural History Specimens. Vol. 1, The Invertebrates." Philosophical Library, Inc., New York. The first volume of what should eventually be the most exhaustive survey of techniques for the collector.

Welch, Paul. 1948. "Limnological Methods." McGraw-Hill Book Company, Blakiston Division, New York. A book on physical and chemical techniques of limnology as well as on biological sampling. A technical book, indispensable to the serious student of fresh waters.

Wing, Leonard. 1951. "Practices of Wildlife Conservation." John Wiley & Sons, Inc., New York. Two chapters of this book are devoted to techniques of wildlife study and management. These chapters warrant the inclusion of the book in this list, for they cover a wide variety of techniques which have extensive application in field biology.

SOURCES OF MAPS

Maps of various kinds are essential to any biological study. The accompanying list may be of value to the student who is unfamiliar with the kinds of maps used for particular purposes and with the places where such maps may be secured. The list progresses from maps on a relatively small scale covering large areas, to maps which give detailed coverage of a small area.

Atlases and Gazetteers: Such books cover the entire world, but the maps are so small as to be of limited value. Good atlases are published by McGraw-Hill Book Company, New York; J. B. Lippincott Company, Philadelphia; Rand McNally & Company, Chicago; and many other publishing houses. Any good library is likely to have a selection of atlases on its reference shelves.

Folding Maps of Countries and Continents: Larger in scale than the maps in atlases, these maps are still of some value in a general survey of an area. Many such maps are available from the National Geographic Association, Washington, D.C.; C. S. Hammond & Co., Inc., New York; and from many other sources.

State Maps: In preparing distributional studies, and for many other purposes, the biologist may need state maps with county lines and other important geographical features clearly demarcated. Such maps are available in various scales from companies which specialize in geographical material, including the McKinley Publishing Co., Philadelphia, and the National Survey Co., Chester, Vt.

State Road Maps: Gasoline companies are the most convenient source of these maps, which vary a great deal in usefulness and accuracy. Some companies publish atlases which include all the states and the provinces of Canada.

County Highway Maps: Ordinary road maps do not include secondary or dirt and gravel roads, which are often of great interest to the biologist. County highway departments, located at the county seat, usually can provide maps which are brought up to date each year, showing the entire county highway system with notes on the condition of the various roads.

Topographic Maps: The U.S. Geological Survey has prepared numerous maps covering most of the country, which are the most valuable maps the biologist can secure. These "top-sheets" are of different scales, but the two most generally available scales are the 15-minute series, most of which are not modern, and the 7½-minute series, many of which are based on surveys made recently. An index map for each state, and for Alaska, Hawaii, and Puerto Rico, can be secured free of charge by writing to the Director, Geological Survey, Washington 25, D.C. From those index maps, individual sheets can be ordered at 30 cents each. For the beginner, an instruction sheet on topographic symbols can be obtained free. These maps show topography by means of contour lines, which can be easily interpreted with a little practice. The newer maps in the 7½-minute series may show wooded areas in green, a feature of great value to biologists.

Soils Maps: The U.S. Department of Agriculture has published large-scale soils maps of many counties. A list of these maps can be secured from the Department. For the biologist who is concerned with the ecology of an area, these maps are useful.

Coastal Maps: The U.S. Coast and Geodetic Survey publishes numerous maps of the shore line and adjacent areas, similar to the topographic sheets mentioned above. Such maps are also available for overseas possessions and dependencies of the United States (see Foreign Maps below).

Aerial Photographs: For certain purposes, large-scale aerial photographs are more useful than maps. Vegetation, condition and extent of bodies of water, and certain other features can be seen clearly on these photographs. Since it requires a good deal of time to prepare maps, aerial photographs may be considerably more up to date than maps of comparable scope. The Armed Forces may have restrictions on the availability of maps of some areas, but aerial photographs of many areas may be obtained through the Soil Conservation Service, which uses them in planning conservation measures for farmers. The county soil conservation agent or Farm Bureau agent can help in securing these photographs if they are available for your area.

Foreign Maps: The traveler to foreign lands may not be content with the continental or country maps in an ordinary atlas. Maps of a scale similar to topographic maps are available for many countries. More complete information than can be given here may be obtained from Olson and Whitmarsh (see below).

1. *Canada.* Numerous maps similar to U.S. Geological Survey topo-

graphic sheets may be obtained from Canada Topographical Survey, Ottawa.

2. *Latin America.* Maps of Mexico in scale of 1:100,000 may be secured from Comision Geografica de Guerra y Fomento, Mexico City. Many of these are out of date. Maps of most parts of Latin America in the scale of 1:1,000,000 have been issued by the American Geographical Society.
3. *United States Possessions and Dependencies.* The U.S. Coast and Geodetic Survey has produced some shore-line maps of Alaska, Guam, Hawaii, the Philippines, and Samoa, which cover most of the areas usually visited.
4. *Other countries.* Road maps of many countries, which may now be somewhat out of date but which are useful in planning itineraries, are included in Atlante Internazionale del Touring Club d'Italiano, available in many libraries.
5. *List of map sources.* Olson, E. C., and Agnes Whitmarsh. 1944. "Foreign Maps." Harper & Row, Publishers, Incorporated, New York. This publication lists major sources of maps for all countries.

SOURCES OF BIOLOGICAL SUPPLIES AND EQUIPMENT

This is by no means an exhaustive list. It includes, however, a sufficient variety of companies to permit the biologist to secure almost any type of standard biological materials.

Carolina Biological Supply Company
Burlington
North Carolina

Cambosco Scientific Company
37 Antwerp Street
Brighton Station
Boston, Mass.
(specializes in botanical supplies)

Central Scientific Company
1700 Irving Park Road
Chicago 13, Ill.

Clay-Adams, Inc.
141 East 25th Street
New York 10, N.Y.

Fisher Scientific Company
633 Greenwich Street
New York 14, N.Y.
(also has branches in major cities of United States and Canada)

General Biological Supply House
8200 South Hoyne Avenue
Chicago 20, Ill.

Hamilton Bell Co., Inc.
610 River Street
Paterson, N.J.

Harvard Apparatus Company, Inc.
Dover, Mass.
(specializes in physiological equipment and instruments)

Jonas Bros., Inc.
Denver, Colo.
(taxidermist's and collector's supplies)

LaPine Scientific Company
6001 South Knox Avenue
Chicago, Ill.

Nuclear Instruments & Accessories, Inc.
150 Fifth Avenue
New York 10, N.Y.
(instruments and supplies for radioactivity studies)

Quivira Specialties Company
4204 West 21st Street
Topeka, Kans.

Standard Scientific Supply Corporation
808 Broadway
New York, N.Y.

The Welch Scientific Company
1515 Sedgwick Street
Chicago 10, Ill.

Will Corporation
New York 52, N.Y.
(also has branch offices in major cities)

Ward's Natural Science Establishment
P. O. Box 1712
Rochester, N.Y.
(West Coast branch at Monterey, Calif.)

Wildlife Supply Company
2200 South Hamilton Street
Saginaw, Mich.
(specializes in equipment for forestry and wildlife studies)

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